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Vegetation of the Northern Part of Cherry County, Nebraska

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VEGETATION OF THE NORTHERN PART
OF CHERRY COUNTY, NEBRASKA*

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VEGETATION OF THE NORTHERN PART OF CHERRY COUNTY, NEBRASKA

INTRODUCTION

Agricultural practices in the Great Plains of North America are now in a period of adjustment from a traditional agriculture initiated by pioneer farmers to a grazing economy based upon potentialities of climate and soil. The attainment of a proper system of land use has been retarded in many localities by the lack of definite information concerning the vegetation and its indicator significance. In this study of the vegetation of Cherry County, Nebraska, the interrelations between the plants and their environments are discussed, the dominant species are described, and changes in grasslands caused by seasons, grazing, and climatic cycles are explained.

Cherry County, which is located in north-central Nebraska, extends from 100°10' to 102°2' west longitude and from 42°7' to 43° north latitude, distances of 96 and 63 miles, respectively. It is the largest county in Nebraska and includes an area of 6,048 square miles. More than 90 percent of this area lies in the sand-hill region. The remainder (the hardlands) consists of fine sandy loam soils, the main body of which is north of the Niobrara River and northeast of Minnechadua Creek.

A study of the vegetation of the sand hills of Nebraska was first made by Pool (1914). Reviews of pioneer work on the taxonomy of various species may be found in his paper. Since then few studies have been made. Weaver (1920) described root systems of certain sand-hill plants, and Keim and Frolik (1932) studied the introduction of exotic legumes and grasses into wet meadows and recorded the effects upon productivity. Ramaley (1939) made a study of the flora of the sand hills of northeastern Colorado and compared it with the sand-hill flora of Nebraska.

According to information obtained from pioneers who are yet living, the dunes were not as well vegetated in the early years of settlement as they are at present. Blowouts were more common, and pioneer vegetation was more prevalent. An early resident stated that sand-hill bluestem (*Andropogon hallii* Hack.) was much more common than it is today. Little bluestem (*Andropogon scoparius* Michx.) was once dominant and led Pool (1913) to describe a "bunch-grass association." Early pictures verify Pool's conclusions (Anderson & Walker 1920) and also indicate that blowout grass (*Redfieldia flexuosa* (Thurb.) Vasey) and weedy plants like soapweed (*Yucca glauca* Nutt.) were once very common.

Changes in vegetation of the sand hills since their settlement by white men have accompanied the control of fires, and differences in land use and intensity of grazing. Before the development of ranching,

prairie fires occurred throughout the region at varying intervals. These fires spread rapidly and generated intense heat wherever sufficient debris had accumulated. Buds were killed, even in the centers of the bunches of grass, and roots were burned. Severe wind erosion followed denudation, and most dunes were permanently capped with a blowout. After each fire pioneer grasses and forbs began a new succession of plants. Only after several years was enough litter again accumulated to feed new fires. Since the beginning of the present century grazing has checked this accumulation, and therefore fires have been under control. Dunes are now held in place and large blowouts are rare. Variation in composition of vegetation is now caused by grazing and local environments.

Areas of vegetation on government preserves or on private ranges which have been protected from both fire and grazing for many years indicate the potentialities of development of vegetation in the several environments. Modifications of composition regularly accompany shifts from one phase of the climatic cycle to another. The decrease of little bluestem during the recent dry years is a striking example.

The writer wishes to acknowledge his indebtedness to Dr. J. E. Weaver, professor of plant ecology at the University of Nebraska, for helpful suggestions and criticisms not only during the progress of this study but also in the presentation of the results. He is also indebted to the Nebraska Conservation and Survey Division, under the direction of Dr. G. E. Condra, for making possible the field studies upon which this report is based. Thanks are extended to Dr. Ward M. Sharp and Mr. Geno Amundsen, both of the United States Biological Survey, for assistance in numerous ways.

GEOLOGY AND SOILS

The controlling factors in development of drainage, topography, and soil lie in the stratigraphy, structure, and texture of the rocks. Sands and limy sandstones were deposited in two formations during Pleiocene times upon the Brule clay of Oligocene age. The Valentine sand formation was deposited to a depth of 75 feet directly above the Brule clay, and this was later capped with a limy sandstone which is called the Ash Hollow formation.

The parent materials of fine sandy loam soils are derived from the Ash Hollow formation. The chief area of such soils is located on the Crookston Table north of the Niobrara River in the northeastern corner of Cherry County. During the Pleistocene and recent times, runoff from these uplands has formed a water-erosion topography of ravines and deep canyons between relatively level tablelands. Water enters readily into dune sands which are located

south of the Niobrara River, and thus there is little runoff from the surface of the dunes. Here wind erosion has played a dominant role in the formation of a rough, irregular dune topography (Fig. 1).



FIG. 1. General view of sand-dune topography; the east end of Dewey Lake is in the background.

Water has eroded valleys and canyons into the sand hills only where its movement attains sufficient velocity and volume to carry a load of sand. The Niobrara River has cut across the sand hills in northern Cherry County and eroded through the Ash Hollow limy sandstone to points below the top of the Brule clay from Valentine eastward (Fig. 2). Tribu-



FIG. 2. General view of Niobrara Valley looking eastward from Fort Niobrara Game Preserve. Deciduous trees grow along the river and on the north slopes. Ponderosa pine is scattered over the mixed prairie grasslands on the south slopes and along the limy sandstone outcrops in the immediate right foreground. A good stand of western needlegrass occurs in the foreground.

aries of the Niobrara River also have eroded canyons and established surface drainage southward toward the interior of the sand hills, but drainage is yet immature in many areas. This results in a high water table which forms lakes in depressions and many acres of grassland are subirrigated in the broad, shallow valleys. Sand hills immediately adjacent to

the deep canyons, however, are well drained and have a water table far beneath the surface. A system of lateral tributaries has not developed on either side of the permanent creeks and streams.

Rain filters directly into dune sands with little or no surface runoff and reaches the water table except as removed by evaporation from the surface of the sand and by absorption and transpiration. The amount of rain that reaches the water table is therefore considerable, especially during years of heavy snow and early spring rain. After the development of vegetation begins in spring, rain seldom falls in amounts sufficient for water to penetrate beyond the reach of the roots of plants. Sufficient water filters through the soils in ravines and along slopes of the canyons, however, to maintain a water table deep beneath the surface.

Streams and lakes in the sand hills constantly receive drainage from the ground water. The streams therefore have a continuous flow throughout the year, and seasonal fluctuations never exceed a few inches. In contrast, the creeks and rivers which receive surface drainage from hardlands are flooded by runoff water during heavy showers.

The Valentine Lakes receive water from springs concentrated along the south and west shores. Poorly drained lakes fluctuate in depth between periods of high rainfall and drought. Lakes with good surface drainage and an abundant supply of spring water do not have marked periodical fluctuations of the water level. Surface drainage prevents an accumulation of large quantities of water during periods of abundant rainfall, and a good supply of water from springs prevents excessive lowering of the level of the lake during drought.

Numerous small springs and seepages occur on the south side of the Niobrara Valley at a point of contact between the impervious Brule clay below and the sandy formations above. These are at the same level as the river near Valentine, but as the river erodes into the Brule clay they occur as much as 125 feet above the valley floor 15 to 20 miles east of Fort Niobrara Game Preserve. Only a small amount of moisture penetrates beyond the depth of plant roots in the fine sandy loam soils of the Crookston Table, and thus only a small quantity of moisture reaches the water table. Seepages have developed north of the Niobrara Valley only near the heads of the major canyons.

The lowest recorded elevation in Cherry County is 2,373 feet above sea level. The rise in elevation from the Niobrara Valley near Valentine southward to 3,001 feet near Kennedy is about 12 feet per mile. Nights are cool throughout the summer because of these elevations.

Little soil formation has taken place in the sand-hill region because of wind erosion. The tops of the dunes have a coarser texture than the sides and adjacent dry meadows due to the selective action of wind erosion. Dune sands have little or no organic matter, but the dry meadows have been stable long enough for the accumulation of small quantities of

humus in the surface few inches. The latter are classified under the Valentine soil series.

In the surface sands in many wet meadows considerable organic matter has accumulated, and deposits of peat are found in old lake beds. Sands of the second and third foot levels have been modified by poor aeration and drainage. These are included under the Gannet soil series. They occur only in meadows adjacent to well drained lakes where the water table does not fluctuate more than 2 to 3 feet. A growth of mesophytic tall grasses occurs in this habitat.

Shores of lakes without surface drainage are subject to great fluctuations in the water table. Vegetation remains permanently in phases of development, and little humus accumulates in the sands.

Salts have accumulated in certain poorly drained wet meadows in sufficient quantity to inhibit all plant growth or all except that of the most salt-tolerant species.

Parent materials on the hardlands areas have undergone varying degrees of development, resulting in dark brown and Chernozem soils. Soils with deep, well developed profiles are found on the flats. These are included in the Holt series. Soils with shallow profiles occur on the low, rolling hills and are classified in the Rosebud series. Soils of considerable variation in texture occur on well drained terraces and hillsides. Mixed prairie grasses grow on the hardlands.

METHODS

Two centers of study were established in eastern Cherry County, one at the Valentine Lakes Refuge, and the other at Fort Niobrara Game Preserve. The former is a typical sand-hill area with poorly drained valleys. Grazing has been discontinued only since 1935, and much of the vegetation is disclimax. Both hardland and well drained sandy habitats are included in the Fort Niobrara Game Preserve. Much of this area has been protected since 1914, and vegetation is near maximum development. Stations were established in all typical types of vegetation in both areas. Work was concentrated at Dewey Lake in the Valentine Lakes Refuge in 1937 and at the Fort Niobrara Game Preserve in 1938.

Environmental data were obtained in prairie and woodland in 1936; in a wet meadow, a dry meadow, and on the south slope of a dune in 1937 and in a dry meadow, a mixed-prairie area, and on both a north and south slope of a dune in 1938. Precipitation records were those of the weather stations at Valentine and the Valentine Lakes Refuge. Measurements of soil moisture to a depth of 5 feet were made at weekly intervals at the various stations during the growing season of 1937 and 1938. Hygroscopic coefficients were obtained from representative samples from the surface 6 inches of soil, except in the wet meadow where samples were taken also at depths of 12 and 24 inches. Percentage of moisture above the hygroscopic coefficient was considered available to plant growth.

Soil and air temperatures at a depth of 3 inches and at a height of 4 inches, respectively, were recorded by thermographs. Relative humidity was measured by hygrographs and evaporation by Livingston's white spherical atmometers, each fitted with a nonabsorbing device. The atmometers were operated in pairs at a height of 3 inches above the soil surface. Readings were made each week and reduced to those of standard atmometers. Anemometers located 6 inches above the surface of the soil recorded wind movement in miles per week. Stakes were driven on the eroding side of a young blowout in the fall of 1937 to ascertain the rate of removal of sand by wind during the winter. Water level was measured by inserting one-inch iron pipes with sandpoints attached, to depths of 4 to 8 feet into the sand. Depth of water level was determined by inserting a weighted tape marked with chalk, which was readily wetted.

The boundaries of the communities included in this study were determined by ocular survey; roots were excavated; diagrams of both aerial and underground parts were made; and several hundred basal area and census quadrats were located at random within the several communities. Basal area was recorded in square centimeters. Bunches or stems of plants were used as units in listing, according to convenience.

ENVIRONMENT

The summer climate of this semiarid region is characterized by a growing season of moderate length, with occasional thundershowers, high daily temperatures, relatively cool nights, low relative humidities, high rates of evaporation, and prevailing south winds. The average frost-free period is 151 days.

The winters are moderately cold, with minimum temperatures as low as -10° to -38° F. Snowfall is light and of little value in restoration of moisture on the tablelands and windswept tops of sand dunes. Much of the snow is blown into low protected places or onto the leeward steep hillsides along the edges of the tablelands. Prevailing winds in winter are from the west and northwest.

PRECIPITATION AND SOIL MOISTURE

The average annual precipitation at Valentine for a period of 51 years, prior to 1938, was 18.3 inches. That during the growing season, April to September inclusive, was 14.9 inches. The great variation in precipitation is illustrated by the average annual rainfall during each of the 4-year periods ending in 1926, 1930, and 1934. The amounts were 17.3, 22.8, and 14.9 inches, respectively. The 3-year period ending in 1937 had an average annual rainfall of 13.4 inches. The year 1929 had a total rainfall of 28.9 inches, and 1937, 11.5 inches.

Rainfall at Valentine in 1935, was 1.5 inches below normal. March and April had a total precipitation of 14.6 inches, which was 4.5 inches above normal. The last half of the year, however, was

unusually dry with a total precipitation of only 2.9 inches, 4.8 inches below normal. This drought period continued through the entire year of 1936 with a total rainfall of only 12.5 inches or 5.9 inches below normal. It did not end until the fall of 1937 when 3.2 inches of rain fell late in August and early in September. Precipitation was plentiful in the spring of 1938 when 4.5 inches more than the normal amount fell from March to May, inclusive. Most of July was dry, but showers late in June and early in July prolonged the growing season. The late summer and entire fall were dry, with rainfall 3.5 inches below normal from June to October, inclusive.

Precipitation data for only 1937 and 1938 are available at the Valentine Lakes Refuge. Here the trend in rainfall was the same as that at Valentine. Both stations recorded 5.6 inches rain from July 1 to September 30, 1938, but at Valentine Lakes Refuge rains occurred in fewer and heavier showers, and were thus more efficient in replenishing soil moisture.

The quantity of available moisture is the most important single environmental factor in determining the composition of plant cover. The total quantity of moisture finally available in any upland environment is determined by the disposition of fallen moisture. This disposition is controlled by soil texture. Slight differences in the efficiency of absorption of rain as affected by soil texture is especially important in this semiarid region because small quantities of moisture determine the survival of vegetation in periods of drought.

The rate of infiltration is especially important because it determines the quantity of runoff. Even the heaviest rains are usually absorbed directly by dune sands, but considerable moisture is lost by runoff from fine sandy loams, especially during heavy thundershowers. The amount of water finally available further depends upon the quantity of moisture lost by evaporation from the surface and the amount lost by percolation deep into the sands beyond the zone of root growth.

Since the moisture holding capacity of sand is relatively low, rain penetrates deeper into sand than in hardland soils. Therefore less moisture is lost by evaporation from the surface of sand than from fine sandy loams.

Sand, which has a low moisture-holding capacity, loses considerable water by percolation beyond the zone of root growth, especially during winter and early spring. But this loss is unimportant because it occurs at a period of high rainfall and cool temperatures. Also vegetation is dormant during much of this period. Once growth and transpiration has passed the prevernal period, however, there is little loss to the water table. Since summer rains are absorbed with great efficiency, a considerable portion of rain falling in summer is available to plant roots in dune sand.

Fine textured soils have a higher moisture holding capacity than sand. Therefore considerable moisture is held in hardland soils from winter and early spring

before transpiration from vegetation becomes great. But the absorption of rain falling in short, heavy showers is relatively inefficient because much water is lost by runoff and evaporation from the surface of the soil. The quantity of moisture available to plant roots from summer rain is small. Once the moisture stored during early spring is exhausted through transpiration, plants on the hardlands undergo long periods of summer drought.

Efficient absorption of rain during the critical months of summer is the controlling factor in distribution of the several kinds of upland dominant grasses of the region.

Data representing moisture content of sand on top of a dune are shown in Figure 3. The sampled areas were dominated by sand-hill muhley (*Muhlenbergia pungens* Thurb.) and hairy grama (*Bouteloua hirsuta* Lag.). Both in 1937 and 1938 available moisture persisted in the third to fifth foot throughout the growing season. Water in the surface 2 feet varied according to occurrence of showers, and the sand remained without available moisture at same level for 7 weeks during 1937, and for 6 consecutive weeks in the first foot in 1938.

The surface 6 inches in blowouts with no vegetation contained little moisture, except for periods immediately following rains, but the sands beneath the surface 6 inches were moist to approximately their field capacity. Moisture was also unavailable in the surface 6 inches of blowout sands with open stands of blowout grass, but the 0.5- to 3-foot level contained 1 to 2 percent available moisture on June 22, 1938, 22 days after the last shower.

Moisture in Valentine sand, with sand reedgrass (*Calamovilfa longifolia* (Hook.) Hack.) and sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), is recorded for 1937 and 1938 in Figure 4. These fine sands with hygroscopic coefficients approximating 2.5 percent did not absorb moisture as efficiently as sand on top of the dunes, but moisture holding capacity was higher. Available moisture was exhausted in the surface foot when samples were taken on July 17, 1936, and (except at two intervals) from June 15 to August 15 in 1937. As a result of good rains early in the summer of 1938, available water persisted in the surface foot until July 18, except during the third week of June. During 1937 available moisture in the 3- to 6-foot level was exhausted beginning the second week in June and in the second-foot level from the first week in July until late in August. Available water was then restored to the surface 3 feet as a result of 2.6 inches of rain. Soil moisture was depleted gradually in the summer of 1938, but persisted within the surface 5 feet until the last week in July; soon after this none was available until September 11.

Pioneer vegetation in blowouts and communities in early phases of development were slow to deplete moisture. It was available throughout the growing season at depths beyond 2 feet, but xerophytic grasses in well developed communities with large leaf and root surfaces readily absorbed available moisture

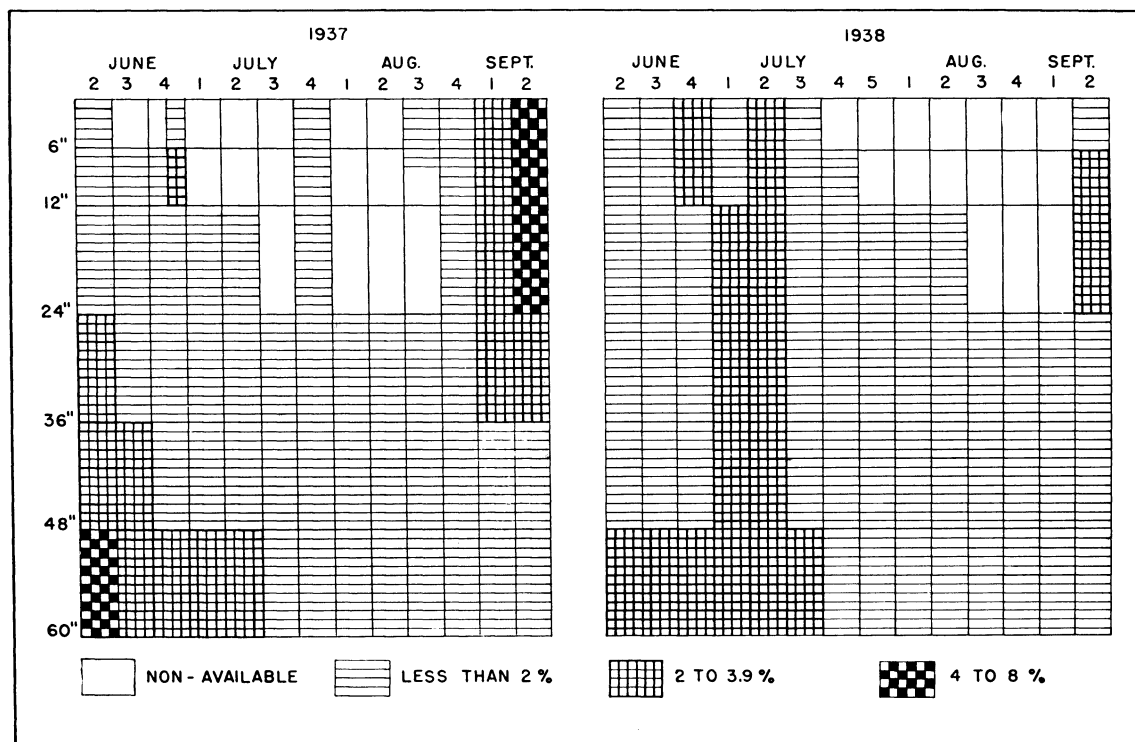


FIG. 3. Available water in the sand on top of a dune in the sand-hill muhley (*Muhlenbergia pungens*)—hairy grama (*Bouteloua gracilis*) community at Valentine Lakes Refuge during the summer of 1937 (left) and at Fort Niobrara Game Preserve (right) during the summer of 1938.

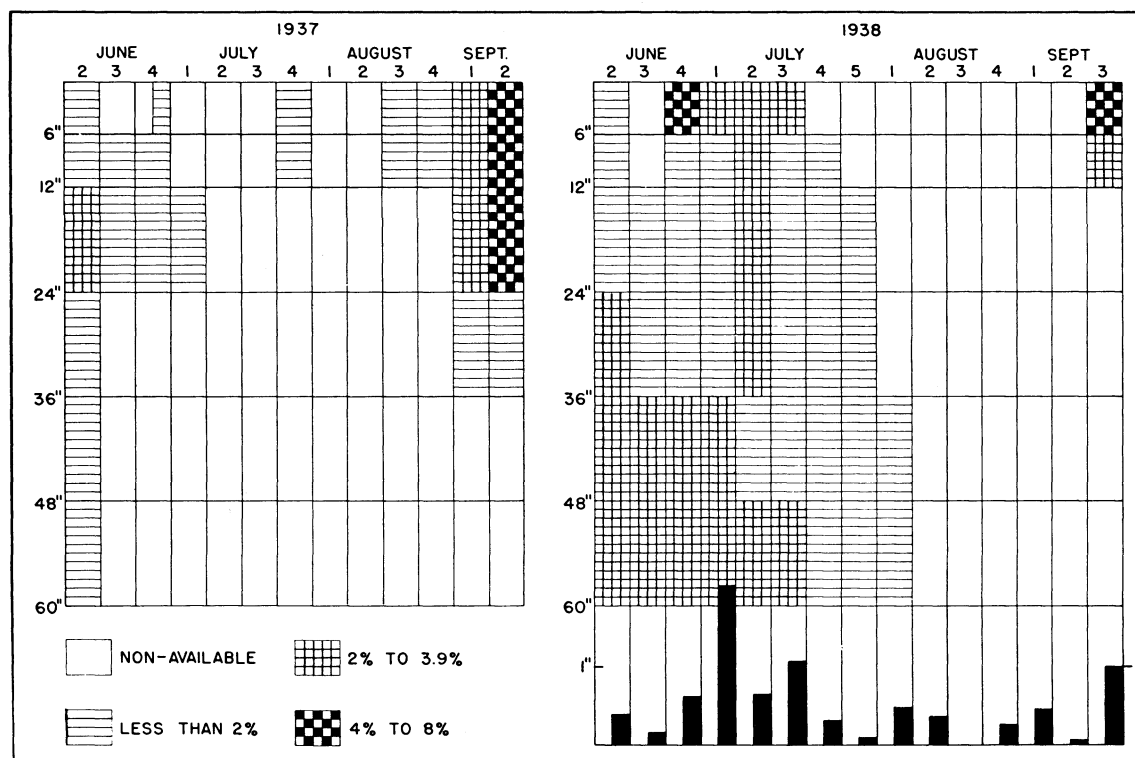


FIG. 4. Available water in Valentine sand in a dry meadow at Dewey Lake in the summer of 1937 (left) and at Fort Niobrara (right) in the summer of 1938. Weekly precipitation for 1938 is shown by vertical bars.

throughout the 4- to 5-foot soil levels and endured long periods of drought.

The efficiency of absorption of summer rain is materially reduced in fine sandy loam, but moisture holding capacity is high. Rainfall of early spring does not penetrate beyond reach of the grass roots, and water from small showers of only 0.2 to 0.4 inch does not penetrate deep enough to reach them. Only the heaviest summer rains are effective in restoring moisture. Available water in Rosebud fine sandy loam is shown in Figure 5. It was present to a depth of

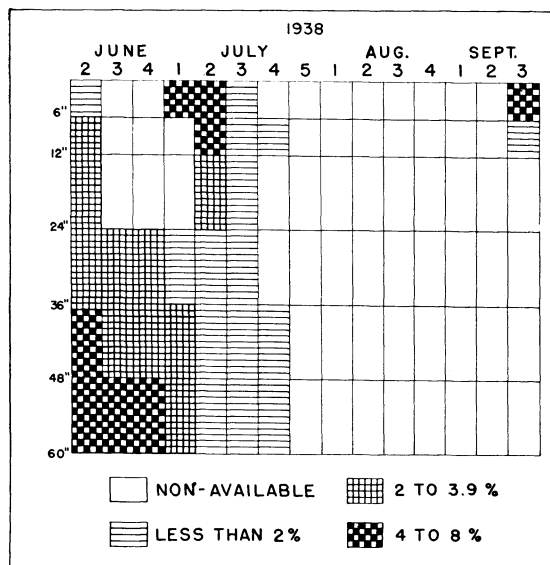


FIG. 5. Available moisture in soil in needlegrass (*Stipa comata*)-niggerwool (*Carex filifolia*) community on hardlands at Fort Niobrara Game Preserve during the summer of 1938.

4.5 feet by May 24, 1938. Soil moisture in this area, which was dominated by needle grass (*Stipa comata* Trin. and Rupr.) and niggerwool (*Carex filifolia* Nutt.), was depleted in the first 2 feet by June 20. Two to eight percent available moisture persisted in the 2- to 5-foot levels. Rain amounting to 1.6 inches fell from June 27 to July 7, replenishing soil moisture in the first 2 feet of soil. Moisture content remained favorable to plant growth until the fourth week in July, but thereafter rainfall was insufficient to replenish it in the surface 6 inches until the second week in September.

Soil moisture in a wet meadow is replenished by rainfall as well as by water from the water table. The supply of ground water is a relatively constant factor, and variations in production in wet meadows from year to year result from differences in rainfall. Water is available throughout the growing season in the lower and middle portions of the wet meadows. It is obtained mostly by plant roots from the capillary fringe immediately above the water table. This extraction causes daily fluctuations of the water table. Roots in the middle portions of the meadow penetrate 2 to 3 feet into the sand where there is the necessary

moisture. On the upper edge of the meadow, however, the rate of growth does not equal the rate of lowering of the water table, especially in late summer and fall. At this time plants endure periods of drought.

Both the surface 6 inches and most lower levels of a Gannet soil at Dewey Lake in 1937 contained available moisture throughout the growing season (Fig. 6).

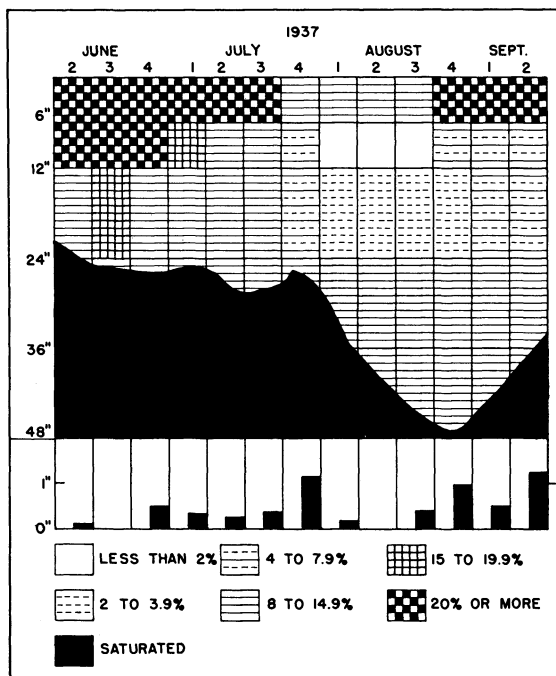


FIG. 6. Available moisture in soil in tall-grass meadow at Dewey Lake during the summer of 1937. Upper edge of the saturated zone (black) is the level of the water table throughout the season. Weekly precipitation in inches is indicated by black bars.

Available moisture in the surface 6 inches was 20 percent or more until July 22, and it never fell below 8 percent throughout the summer. The 6- to 12-inch level contained less available moisture and there was a continuous reduction of water content until heavy rains fell in the autumn. Field capacity was low in the 2- and 3-foot levels, since there was little humus or silt in the sands. Hygroscopic coefficients averaged 2.5 percent. Moisture approached field capacity immediately above the water table throughout the growing season. In an adjacent dry meadow capillary moisture was 23 to 24 inches above the water table on October 25, 1937, but in the wet meadow, such heights were not attained because of absorption by plants.

WATER TABLE AND SALT CONCENTRATIONS

The water table is subject to periodical, seasonal, and daily fluctuations. Periodical fluctuations result from cyclic occurrence of excessive or deficient precipitation in association with poor drainage. The water table at Dads Lake, where there is no surface

drainage, was nearly 8 feet below its usual level in the autumn of 1938. The water table at Dewey Lake, where surface drainage is well established, did not fluctuate more than a few feet over a period of several years. It was kept nearly normal during periods of high rainfall by surface drainage, and during drought, extreme lowering of the water level was prevented by abundant seepage and water from springs.

Seasonal fluctuations of the water table are determined by the amount of rainfall, by replenishment from the water table through springs and seepage, by loss through transpiration, and by evaporation from the lake. The water table in a wet meadow at Dewey Lake fell 1.61 feet from July 7 to August 20, 1937. It rose 0.83 feet as a result of rains in August and September, but again receded to former levels during late September, and did not return to the July level until October 22. Seasonal rise and fall of the water table is represented in Figure 6, where the zone of saturated sand is indicated. The water table fell 2.78 feet from June 30 to September 1, 1938.

Daily fluctuations of the water table regularly occur during the growing season. These fluctuations result chiefly from the quantity of moisture lost by transpiration and the rate of replenishment. Greatest fluctuations occur in the tall-grass meadow.

Water table in a tall-grass meadow near Dewey Lake fluctuated 4.4 inches during a hot, windy day (July 7) in 1937 (Fig. 7). Under moderate conditions, it fluctuated 2.3 inches on August 5, 1937, and 1.5 inches on August 12. Under conditions of high humidity, low wind, and moderate temperature on August 20, the water table fell only 0.3 inch. Fluctuation of the water table 8 feet beneath the surface of a dry meadow at Dewey Lake was 0.6 inch on August 12 and 20, 0.5 inch on September 10 and 0.2 inch on September 28. It was not determined whether these fluctuations were due to transpiration or were the result of variations in water levels in the wet meadow 100 yards distant.

During very dry weather, the most rapid lowering of the water table occurred in the morning, gradually leveling off until four to five o'clock in the afternoon after which it began to rise. During the night, it attained approximately the same level as that of the preceding morning.

Spring and river waters contain low concentrations of soluble salts. A single sample of spring water had 122.1 parts of soluble salts per million of water (ppm.). These waters present a habitat with a flora considerably different from lake waters which have a higher salt content. Salt concentrations differ from lake to lake according to drainage. Beaver, Red Deer, Hackberry, and Dewey Lakes have good surface drainage, and moderate contents of soluble salts (Beaver Lake has 235.8 ppm.). These lakes have a luxuriant growth of various pondweeds. Growth of seed plants, however, is completely inhibited in Clear Lake (13,503.1 ppm.) and in Alkali Lake, where salts have accumulated over long periods of time as a result of high evaporation, abundant run-in water, and

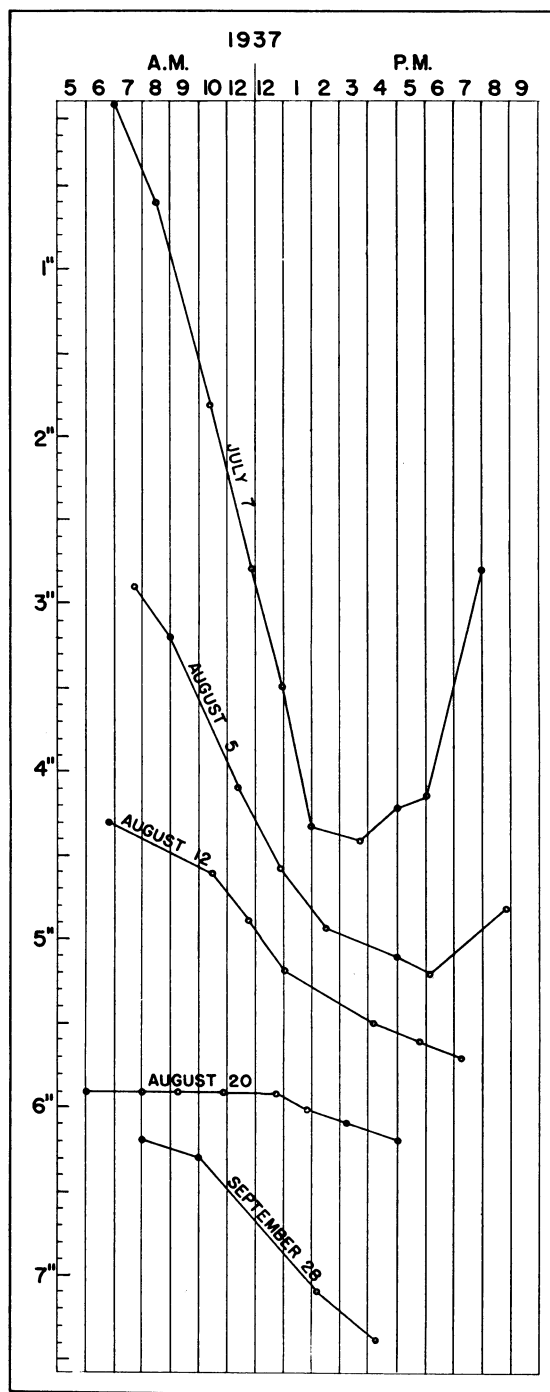


FIG. 7. Graphs showing daily fluctuations of water table in tall-grass meadow near Dewey Lake at various times during the summer of 1937.

poor drainage. High concentrations of salt, however, occur only in the lake body itself. The ground water deep beneath the bed of the lake and under the lake shores has little salt accumulation (282.9 ppm. at Dads Lake).

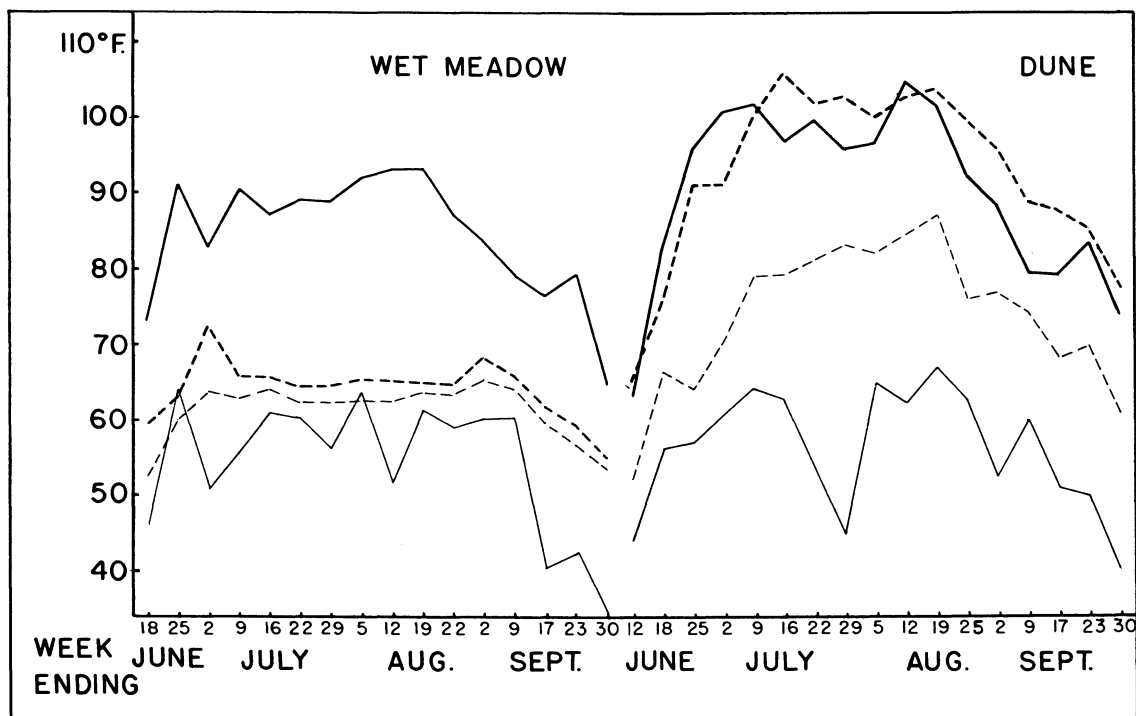


FIG. 8. Summary of average weekly minimum and maximum air temperatures three inches above the soil surface and soil temperature three inches below the surface from a wet meadow and the south slope of a dune at Valentine Lakes Refuge in 1937, respectively. Continuous lines indicate air temperatures and broken lines, soil temperatures.

TEMPERATURE OF AIR AND SOIL

Daily maximum and minimum soil and air temperatures averaged by weeks are recorded in Figure 8. Highest temperatures occurred from the first week in July to the middle of August. Average weekly maximum temperatures above 95° F. persisted for 9 weeks in both 1936 and 1937, but for only 5 weeks in 1938. There were 5 weeks in 1936 with average maximum temperatures above 100° F., but only 2 weeks in 1938. Maximum temperatures ranged from 100° to 115° F. Average maximum temperature of the mixed prairie from May to September, 1936, was 96°, and from May 20 to Sept. 9, 1938, it was 87° F. On the south-facing slope of a dune, from June 12 to Sept. 30, 1937, the average maximum temperature was 87.7°, and from May 20 to Sept. 9, 1938, it was 88.5° F. During 1938, temperatures were approximately the same on the south side of the dune and in the mixed prairie, but the mixed prairie had lower average temperatures during rainy periods.

Average daily maximum temperatures in a grove in 1936 and in a wet meadow in 1937 were persistently lower than those of the mixed prairie and the south side of a dune. Differences as great as 12° F. were recorded in average maximum daily temperatures between woodlands and mixed prairie areas in 1936, and 19° between the wet meadow and the south slope of a dune in 1937.

Night temperatures were low, and during the warm-

est periods, they were seldom high enough to be uncomfortable. Average minimum temperatures on the dune from June 12 to September 30, 1937, and from May 20 to September 9, 1938, were 54.4° and 60.9° F., respectively. Those of the mixed prairie in 1936 were 59.7° and 61.5° F. in 1938.

In uplands, maximum soil temperature was usually slightly below maximum air temperature, but the depression of minimum soil temperatures during the summer was never as great as that of the air. Average maximum weekly soil temperatures on dune from May 20 to September 9, 1937, and from June 12 to September 23, 1938, were 91.3° and 87.5° F., respectively. Those in the wet meadow in 1937 were 64.2° and 61.8° F. Average differences between minimum and maximum air temperatures on the dune in 1937 were 11.7° F. and in the wet meadow, 2.4° F.

RELATIVE HUMIDITY

Average maximum humidity for 12 weeks (from June 18 to September 9, 1937) on the dune and in the wet meadow was 73.9 and 83.7 percent, respectively. Greater humidity in the wet meadow was largely the result of high transpiration by the tall grasses. Low relative humidity occurred in midsummer with high temperatures and drought.

Average maximum relative humidity for 12 weeks (from June 3 to August 26, 1938) on the dune and in the mixed prairie was 71 and 72 percent respec-

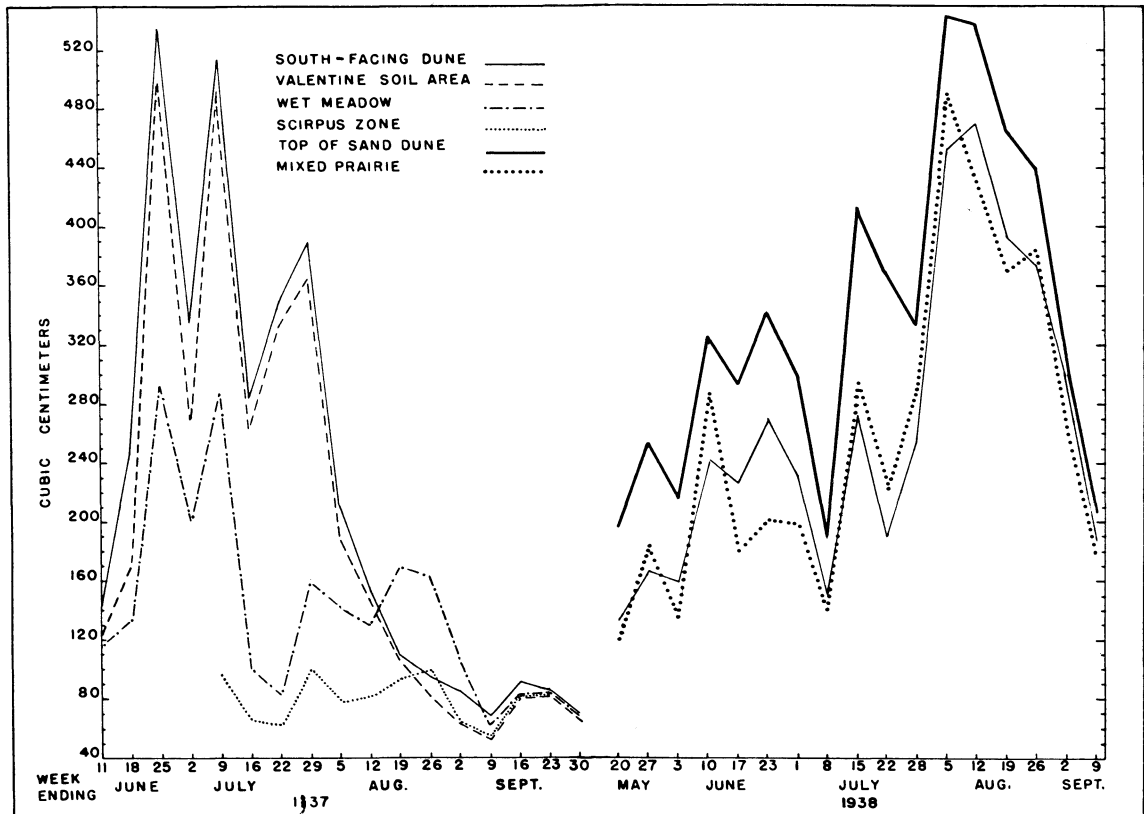


FIG. 9. Weekly rates of evaporation in several sand-hill and hardland habitats during the summers of 1937 and 1938.

tively. Average minimum humidity in the same sequence was 36 and 34 percent. Humidity was higher in the mixed prairie than in that of the dune immediately after a rain because more water evaporated from the soil on the hardlands. Average relative humidity in the several habitats at 3 P.M., June 22 to July 8, 1936, was as follows: sedge meadow, 34 percent; tall-grass meadow, 31; grove of hackberry trees, 26; and south slope of dune, 23 percent.

EVAPORATION

Weekly rates of evaporation in 1937 and 1938 are summarized in Figure 9. Average daily evaporation in 1937 on the south slope of a dune was 33.7 cc.; in dry meadow, 26.0; and in wet meadow, 19.0 cc. Evaporation in the swamp was least, with an average daily rate of 12.4 cc. Average daily evaporation during 1938 on the south slope of a dune was 37.2 cc.; on a north slope it was 29.5 cc.; and on the top 46.9 cc. Evaporation on the mixed prairie was nearly the same as that on the south slope of the dune with an average of 37 cc. Evaporation was highest on the top of the dune where currents of air moved unimpeded in all directions. High rates of evaporation occurred during periods of drought. Reduced evaporation during the last two weeks in August in both 1937 and 1938 was the result of rainfall and seasonal

decrease in temperatures. Evaporation in the mixed prairie habitat was lower than that on the south slope of the dune during rainy periods. The prairie, however, had a more severe aerial environment than did the south slope of the dune during periods of drought.

WIND

Greatest wind erosion occurs during winter. Blowouts develop on the northwest side of a dune, and deposition is on the southeast side. The height to which winds blow the sand is limited and seldom exceeds 50 feet. In a blowout at Dewey Lake, the major wind movement was around the southeast side of the highest point rather than upward and over the dune. The sides of a young blowout are steep, but as erosion continues the dune becomes streamlined, permitting movement of wind over an elevation with a minimum of friction. Stakes driven on the eroding side of a young blowout in the fall marked the removal of 9 inches of sand during the winter of 1937-38.

Plants cannot revegetate a denuded area where wind erosion is severe. A complete cover of vegetation is possible only when the blowout has matured. Erosion increases when the cover of vegetation is destroyed by heavy grazing, and deposits of fine sand

are made in the meadows. Though the effects of this deposition are not immediately noticed, many wet meadows have been filled with 8 to 10 feet of fine sand in relatively recent times, as is indicated by many layers of soil buried deep beneath deposits of fine sand. Blowouts often develop when vegetation is weakened by grazing and trampling. This is especially evident around watering places everywhere in the hills.

Woodlands have a marked effect upon wind velocity, but in grassland, topography is more important in creating local differences in wind movement than is vegetative cover. During 1937, average weekly wind movement on the mixed prairie was 608 miles, but in the woodlands only 76 miles. Extremes on the mixed prairie varied from 482 to 857 miles per week, and at the woodland station 44 to 112 miles. Wind velocity was greater at the tops of dunes than elsewhere, and had a marked effect upon composition of the vegetation. Wind movement on the south side of a dune in 1937 averaged 324 miles per week; in a wet meadow the average was 288 miles. During 1938 on the south slope of a dune the average was 295 miles, and on the mixed prairie it was 272 miles. Extremes of weekly average wind movement on the south side of a dune in 1937 ranged from 105 to 728 miles and in 1938, from 102 to 504 miles. On the mixed prairie in 1938, weekly wind movement varied from 143 to 544 miles.

LIGHT

Full sunlight at 2 P.M. late in summer was somewhat more than 10,000 foot candles. Approximately, only 1 percent of the total sunshine reached the soil in the tall-grass community and only 6 percent was recorded at a foot above the soil surface. Nowhere in the mixed prairie or on the dunes during drought years was light sufficiently low to retard plant growth; but with abundant moisture, tall grasses shaded the shorter ones considerably.

More sunlight reached the soil covered with swamp vegetation than the soil in the tall-grass meadow. An average of several readings in a dense stand of arrowhead was 15 percent of full sunlight; it was 17 percent in a mixture of arrowhead and western bulrush. In the common reed zone with an underlayer of arrowheads, light intensity was the same as that near the soil surface in the tall-grass zone. In pure stands of common reed, intensities of 2.8 to 5 percent were recorded at the surface, and 5 feet above the ground readings ranged from 8 to 24 percent.

Light values in shade of hackberry trees approximated 3 percent of full sunshine; in a willow thicket, 0.1 percent; and in a plum thicket, 2.6 percent.

GENERAL DISTRIBUTION OF VEGETATION

Cherry County is a great tract of sand-hill grassland. This is some of the best range land in the United States. The great monotony of rolling dunes and waving grass is occasionally broken by a broad,

shallow valley. Here large areas of tall-grass meadow stand in contrast to smaller ones of dark-green swamp or shallow lake. Sometimes there is a grove of cottonwoods planted by the pioneers. Hardland and river-valley habitats are of minor importance, but of great interest since they have an entirely different vegetation.

The various plant communities are distributed largely according to the quantity of water available to vegetation. They are therefore described in order of succession from the submerged plants in lakes and ponds to the climax communities on the hardlands. Intermediate groups include communities of swamps, wet meadows, and sand dunes. Postclimax woodland and chaparral are present in the river valleys. The xerosere is almost absent.

Submerged and floating vascular plants grow in the lakes and ponds. Emerged hydrophytes occur in shallow water along the protected shores. There are also several characteristic hydrophytes in swamps where peat has accumulated in large quantities. Mesophytic grasses grow in the subirrigated meadows, which are conveniently divided into three zones. A lower zone, usually flooded in spring, has a growth of sedges and hydrophytic grasses. The tall grasses dominate a middle zone, and the xerophytic plants of the true prairie occur on the upper edge of the meadow where vegetation undergoes periods of drought, especially in late summer. Halophytes are present in saline meadows.

Postclimax tall grasses grow in the dune sands. Pioneer grasses are characteristic of the blowouts. As the communities mature the pioneers are succeeded by more xerophytic dominants. In the final communities, resulting from decrease in moisture, the dominants are distributed in several alternates according to minor differences in environment. Growth of tall grasses is retarded or prevented by the extreme aerial environment on top of the dunes where short grasses are dominant. Certain tall grasses occur mainly on the south slopes of dunes; others are present mainly on the north slopes. Marked changes in composition of vegetation are caused by grazing.

Mid and short grasses of the mixed prairie association occur on the hardlands, where they develop as the climax vegetation. Here also the several major species occur in communities distributed according to minor differences in environment, or composition is modified by different intensities of grazing.

Deciduous trees and shrubs form woodland and chaparral in well drained, subirrigated areas along streams, bottoms of deep canyons, and other habitats favorable to postclimax arboreal species. Groves of ponderosa pine occur on rough, stony land in the deep valleys.

HYDROPHYTIC COMMUNITIES

PLANTS SUBMERGED OR WITH FLOATING LEAVES

Submerged and floating species are found in fresh-water lakes and in ponds formed by dams

across small streams. Several species grow from the edge of the permanent water line far into the shallow lakes. Submerged plants are able to withstand wave movement and therefore occur throughout the lakes except as inhibited by unfavorable depths, excessive saline content of water, or extremes of wave movement along unprotected, sandy shores. Near the edge of the permanent water line of protected lagoons, submerged plants become more common than the floating species.

Among the common submerged species are five pondweeds, namely, *Potamogeton pectinatus* L., *P. natans* L., *P. richardsonii* (Benn.) Rydb., *P. zosteriformis* Fernald, and *P. foliosus* Raf. Hydrophytes equally as common are coontail (*Ceratophyllum demersum* L.) and milfoil (*Myriophyllum spicatum* L.).

Other pondweeds (*Potamogeton praelongus* Wulfen., *P. angustifolius* Berch. & Presl., **P. strictifolius* A. Benn.) are of less common occurrence since they grow mainly in fresh water. Other members of this group are *Najas flexilis* (Willd.) Rostk. & Schmidt., *Ranunculus delphinifolius* Torr., **Batrachium divaricatum* (Schrank) Wimmer, *Lemna trisulca* L., *Wolffia columbiana* Karst., **Elodea canadensis* Michx., and *Utricularia minor* L.

Floating and partially submerged plants which are unable to withstand severe wave movement form small communities in well protected areas. The broad-leaved pondweeds and yellow cow lily (*Nuphar advenum* Ait.) are the most common constituents of such communities. The yellow cow lily, which may occur in colonies of several square yards, spreads by means of starch-laden rhizomes several inches in diameter. It has floating and emersed leaves and flower heads that usually extend well out of the water. White water lily (*Nymphaea odorata* Ait.) has been introduced in some localities. *Polygonum*

* Species marked with an asterisk are found only in water with little salt in solution.



FIG. 10. Transition zone between communities of wild rice (*Zizania aquatica*) and cattail (*Typha latifolia*), with yellow cow lily (*Nuphar advenum*) in the center. Tops of the swamp willow (*Salix petiolaris*) appear in the background above the wild rice.

amphibium L. occurs in a few places, and duckweed (*Lemna minor* L.) floats in masses upon quiet waters.

Wild rice (*Zizania aquatica* Hitchc.) is a pioneer annual species. It grows in small, protected lagoons of only a few acres where depth of water does not exceed 2 to 3 feet in the early part of the growing season (Fig. 10). It germinates under water, passes through a submerged and floating stage, and finally emerges during July and August. The plants grow 2 to 4 feet high where aeration of the soil is poor, but attain a height of 7 to 8 feet where the water table is several inches beneath the surface. Under such conditions a single plant may spread over as much as 4 square meters and produce 25 culms. Seeds fall to the ground immediately upon ripening and are a valuable food for aquatic fowl. Wild rice is not successful in competition with established marsh vegetation or annual weedy plants which germinate along the exposed lake shores when water levels fall in June and early July. Neither is it capable of surviving in open, shallow waters where the plants are subjected to the full force of wind and wave movement.

SPECIES OF THE SWAMPS

Emergent plants form well defined zones from the edge of the permanent water line to the lower margin of the tall-grass meadow. This zonation is the result of differences in the ability of the several swamp plants to withstand deficiency of oxygen. The level of the water table and time of submergence of surface soils directly affect the quantity of oxygen available to plant roots. The common species of the swamp are able to withstand fluctuations of the water table of approximately 3 feet, but they vary among themselves in survival when flooded. Common reed (*Phragmites communis* Trin.) is least able to grow in deep water, and western bulrush (*Scirpus acutus* Muhl.), swamp sedge (*Carex lacustris* Willd.), cattail (*Typha latifolia* L.), and arrowhead (*Sagittaria latifolia* Willd.) are increasingly able to grow in deep water in order named.

Depth of the water table in June and September in the various swamp zones at Dewey Lake is shown in Table 1. The upper portion of the swamp was flooded only during the early part of the growing sea-

TABLE 1. Depth of water table expressed in feet (') and inches (") in various plant zones at Dewey Lake in 1938.

Community	Distance of level of water from the surface	
	June 7, 1938	Sept. 21, 1938
Wild rice—cow lily zone	3" above	¼" above
Wild rice—cattail transition	2' 9" above	1" below
Cattail—Scirpus transition	2' 7" above	2" below
Near center of the Scirpus zone	1' 1" above	1' 8" below
Scirpus—sedge meadow transition	At surface	2' 4" below
Sedge meadow—tall-grass transition	11" below	2' 11" below
Tall grass—true prairie transition	2' 7" below	4' 9" below
True prairie—dune tall grass transition	4' 1" below	6' 3" below
Dune tall-grass community	5' 10" below	8' below

son, but the arrowhead-cattail zone immediately adjacent to the permanent water line was flooded throughout the summer. The range of elevation from highest to lowest levels of the swamp at Dewey Lake was 28 inches. The water table fluctuated nearly 3 feet from spring to fall.

Arrowheads grew in nearly pure stands and formed communities with cattails on the lower edge of the swamp near the permanent water line (Fig. 11).



FIG. 11. Arrowhead (*Sagittaria latifolia*) with pondweeds (*Potamogeton* sp.) and duckweed (*Lemna minor*) floating on the water in a pond near Valentine.

They also formed a ground layer in the bulrush and common reed communities at higher levels. They were good pioneers along shores made bare by receding water levels. Here they grew from seed and produced flowers in two months. At Dewey Lake they withstood 2 to 3 feet of flooding in late May and early June. Floating leaves were present when water levels were high, but emergent leaves developed as the water table lowered. Large white flowers appeared late in June, and seeds soon matured on the pistillate inflorescences. Fleshy tubers formed late in summer, 4 to 6 inches beneath the surface. The leaves turned yellow, and the plants became dormant long before killing frosts.

Cattails are not as common as arrowhead along the lake shores. *Typha* formed colonies among the arrowheads in the lower portions of the swamp and occurred in all the hydrophytic communities. *Typha*

spreads by rhizomes 8 to 10 inches in length and forms dense, compact stands under optimum environments.

Carex lacustris, also spreading by rhizomes, sometimes formed communities of several acres but more commonly they covered only a few square yards. Few other species occurred, but occasional plants of *Urtica* sp. and *Polygonum coccineum* Muhl. were present. This sedge grows in small bunches with a basal area of approximately one square decimeter. The stems are triangular with dark green, shiny leaves. Height varied from 36 to 56 inches. Flowering stalks rarely developed. Occurrence of this sedge only in the portions of the swamp where there were many springs indicated its intolerance of salinity.

Western bulrush dominated the upper portions of the swamp where maximum water table levels flooded the surface of the peaty soil from a few inches to 3.6 feet in depth. It withstood an annual fluctuation of the water table of 3 feet, and was also tolerant of moderately saline water. At Dewey Lake it dominated several acres but occurred sparingly in communities of cattail and common reed. Bulrush propagated by rhizomes a few inches to 6 feet in length, from which cylindrical culms arose every few inches. These attained a height of 4 to 6 feet. Growth began during the first week in May, 1938, and during the first week in June the stems were 3 to 4 feet tall. Inflorescences developed near the top of the stalk late in May.

Common reed grew in large colonies on the upper portions of the western bulrush zone. During periods when the water table was low it spread rapidly by extensive rhizomes, some of which attained a length of 30 feet. Culms appeared at intervals varying from 6 to 18 inches. Maximum spread was made during 1937, but under the influence of high water levels during 1938, the common reed zone receded 8 to 10 feet along the lakeward side. Growth began in the middle of May, 1938; by the first week in June culms were 30 to 36 inches tall, and each had 5 to 6 leaves. By the end of June the plants attained a height of 72 inches, and each had 12 to 13 leaves. Flowers developed on culms 7 to 8 feet high during the second week in August. In late summer the lower leaves turned yellow and fell to the ground. Widely spaced plants of arrowhead and western bulrush grew beneath the common reed.

PLANTS ABOUT SPRINGS

In the Niobrara Valley and along the shores of a few sand-hill lakes, especially those at the source of streams, are areas which are well drained and supplied with a fairly constant flow of fresh, cool water. Here the water table fluctuates but little. Much organic matter has accumulated in the moist sands. Such habitats support a large number of species of limited importance.

Scirpus fluviatilis (Torr.) A. Gray, *S. validus* Vahl., *Alisma subcordatum* Raf., and *Sparganium eurycarpum* Engelm. are found in the more hydrophytic areas where fluctuations of the water table

are moderate (6 to 18 inches). Sedges and hydrophytic grasses dominate the few small swamps where the water table is just beneath the surface and where it does not fluctuate more than a few inches throughout the year. The most important of these are *Carex hystricina* Muhl. and *Glyceria nervata* (Willd.) Trin. Others occur rarely, and may be regarded as relicts. Twenty-five such species were observed.

Among the annual plants found where the perennial grasses and sedges had been destroyed by grazing were *Echinochloa crusgalli* (L.) Beauv., *Leersia oryzoides* (L.) Swartz, *Bidens cernua* L., *Lobelia siphilitica* L., *Gerardia tenuifolia parviflora* Nutt., *Impatiens biflora* Walt., and *Mimulus ringens* L.

PLANTS OF PEAT SOILS

Peat soils with a permanent water table 6 to 12 inches beneath the surface are dominated by swamp willow (*Salix petiolaris* Smith) and marsh fern (*Thelypteris palustris* Schott.). Forbs and grasses of secondary importance are *Aster umbellatus* Mill., *Calamagrostis canadensis* (Michx.) Beauv., *Eupatorium maculatum* L., *Impatiens biflora*, *Triadenum virginicum* (L.) Raf., *Mentha canadensis* L., *Lycopus hispida* Pursh., *Polygonum coccineum*, *Phragmites communis*, *Glyceria grandis* S. Wats., *Cicuta maculata* L., *Rumex patientia* L., *Carex lacustris*.

Several forbs increased greatly in the higher portions of the community during 1937 and 1938 where the water levels become lower during the severe drought. These were *Aster nebraskensis* Britton, *Oenothera hookeri* T. & G., *Helianthus grosseserratus* Martens, *Solidago serotina* Ait., and *S. altissima* L. In the lower portions of the community the pioneer forbs, *Rumex patientia*, *Epilobium densum* Raf., *Ludwigia polycarpa* Short and Peter, and *Alisma subcordatum* also increased.

During 1937 water levels fell rapidly in the Valentine Lakes leaving bare areas of peat open to invasion. As soon as the water table receded beneath the surface, annual forbs began to grow. Even after August first, seedlings of *Chenopodium rubrum* L. grew in dense stands, and attained heights from 6 to 24 inches, depending upon their age. Several hundred acres of pure stands of this species grew in the lake beds of White Water, Pelican, Willow, and Marsh Lakes during 1937. Water levels, however, were sufficiently high during 1938 to inhibit germination over much of the area formerly occupied. *Chenopodium album* L. grew in pure stands on shores which were exposed by receding water levels in early summer, and dominated areas occupied by Typha, Sagittaria, and Scirpus during 1936. *Bidens cernua* formed extensive communities on the shores of Hackberry Lake during 1938. In addition, there were various mixtures of *Polygonum pennsylvanicum* L., *P. lapathifolium* L., *Acnida* sp., and *Panicum capillare* L.

OTHER FRESH-WATER HABITATS

Certain hydrophytic plants, including *Veronica americana* Schwein., *Mimulus glabratus fremontii*

(Benth.) Grant., *Nasturtium officinale* R. Br., *Catabrosa aquatica* (L.) Beauv., and *Berula erecta* (Huds.) Coville, grew partially submerged with roots established in banks along the edges of the small, spring-fed streams where flow and temperatures of water were fairly constant throughout the year.

Shallow depressions on hardlands known locally as "buffalo wallows" are usually filled with water until early summer. Submerged and floating plants such as *Macuillamia rotundifolia* (Michx.) Raf., *Marsilea vestita* Hook. & Grev., and *Eleocharis macrostachya* Britton, are found in these places. They make a rapid growth and produce seeds or sporocarps before the pools are dry in summer.

SPECIES TOLERANT TO SALT

Depth to water table is a conditioning factor in saline habitats. Salt bulrush (*Scirpus americanus* Pers.) grows on the sandy shores immediately above the water table. Salt grass (*Distichlis stricta* (Torr.) Rydb.) develops best at levels 1 to 3 feet higher, and western wheatgrass (*Agropyron smithii* Rydb.) dominates moderately saline soils not influenced by flooding. Grasses and grasslike plants of secondary importance are *Juncus balticus* Willd., *Scirpus acutus*, *Hordeum jubatum* L., *Calamovilfa longifolia*, *Panicum virgatum* L., *Muhlenbergia asperifolia* (Nees and Mey.) Parodi., *Spartina gracilis* Trin., and *Carex siccata* Dewey. Herbs in such habitats are *Ambrosia coronopifolia* T. & G., *Suaeda depressa* (Pursh) S. Wats., *Leptochloa fascicularis* (Lam.) A. Gray, *Helianthus petiolaris* Nutt., *Leptilon canadense* (L.) Britton, *Polygonum ramosissimum* Michx., *Panicum capillare*, and *Salsola pestifer* A. Nels.

Plants tolerant of salts also dominate shores of saline lakes where ground water has a very low salt content, but where marked fluctuations of periodical water levels occur as a result of poor surface drainage. Here the bunch grasses do not become established, and the annual forbs and perennial plants which propagate rapidly by long rhizomes are dominant.

Salt bulrush at Dads Lake extended from the water's edge to levels where the water table was approximately 6 feet beneath the surface. Along the lower limits of the community the plants made a rapid growth and spread by thickened rhizomes 4 to 10 inches in length over areas of several square yards. The tender, dark green leaves reached a height of 12 to 18 inches. In two meter quadrats the number of leaves averaged 765. At the upper limit of the community, growth was much less, the leaves dried in late summer, and no seed developed. Competition with annual and perennial plants was great.

Salt grass is at its best where water levels are 16 to 36 inches beneath the surface of the sand. It grows in nearly pure stands in saline meadows adjacent to poorly drained lakes. It is a pioneer on lake shores from near the edge of the minimum annual water line outward to places 6 to 8 feet above minimum water tables. It is also present in small

quantities in tall-grass meadows. Salt grass grows 2 to 8 inches in height, and spreads by long rhizomes (Fig. 12). A single meter quadrat had 2,616 stems.



FIG. 12. Salt grass (*Dictichlis stricta*) along shores of Clear Lake depicting manner of advance of plants into bare areas by rhizomes from a central, established colony.

COMMUNITIES OF MESOPHYTIC TALL GRASSES

Mesophytic tall-grass communities dominate lands where the capillary fringe above the water table is within reach of grass roots. Such conditions are found in sand-hill valleys adjacent to well drained, fresh-water lakes and along streams. Composition of meadows is modified by soil aeration, by depth to the water table, and by such coactions as grazing and mowing (Fig. 13). Growth of the mesophytic tall



FIG. 13. General view of wet meadow near Merriman, with ranch house and stacks of hay in immediate foreground and sand-hill range in distant background.

grasses is inhibited by great fluctuations of the water table and high saline content of ground water or soil.

The wet meadow has three zones of vegetation. A zone along its lower edge is flooded during the early part of the growing season. A second, more mesic zone is never flooded, but the plants always have access to ground water 2 to 3 feet beneath the sur-

face. A third zone along the upper edge of the meadow receives moisture from the capillary fringe only during the early part of the growing season. Here plants endure periods of drought in summer and fall.

HYDROPHYTIC GRASS AND SEDGE ZONE

The lower zone was dominated by bluejoint (*Calamagrostis canadensis*) and Sartwell's sedge (*Carex sartwellii* Dewey). Less abundant grasses and sedges were *Phalaris arundinacea* L., *Scirpus americanus*, *Hordeum jubatum*, *Carex lanuginosa* Michx., *C. scoparia* Schkuhr., *C. nebraskensis* Dewey, and *C. praegracilis* W. Boott. The width of the zone varied from a few feet to 30 or more, depending upon the slope of the land adjacent to the lake or stream. At Dewey Lake the zone was flooded to a depth of 4 to 6 inches in spring. During 1938 minimum water levels ranged from 2.5 feet beneath the surface at its lower edge to 3 feet at the upper margin of the zone.

Forbs occurred only in small numbers. They were *Asclepias incarnata* L., *Lycopus velutinus* Rydb., *Triglochin maritima* L., *Cicuta maculata*, *Bidens aristosa* (Michx.) Britton, *Aster salicifolius* Lam., *Scutellaria epilobifolia* A. Hamilt., *Helianthus grosseserratus*, *Polygonum coccineum*, and *Stachys scopulorum* Greene.

MESOPHYTIC TALL-GRASS ZONE

The middle portion of the wet meadow was occupied by big bluestem (*Andropogon furcatus* Muhl.)-Indian grass (*Sorghastrum nutans* (L.) Nash) community. The major grasses, listed in approximate order of their occurrence in increasingly less mesic habitats, were slough grass (*Spartina pectinata* Link), switchgrass (*Panicum virgatum*), Indian grass, and big bluestem. This community was found extensively in all the sand-hill valleys where maximum water table levels ranged from 0.9 to 2.3 feet beneath the surface, and minimum levels, from 2.9 to 4.9 feet. Optimum levels were at depths of 1.5 to 3 feet. Active growth in the tall-grass meadow began the first week in May in 1938. Bluejoint, redbop (*Agrostis alba* L.), and slough grass had attained heights of 4 to 6 inches, and Indian grass, big bluestem, and switchgrass were 2 to 3 inches tall by June 6. The average height of the tall grasses late in June was 10 to 12 inches. Timothy (*Phleum pratense* L.), redbop, and slender wheatgrass (*Agropyron pauciflorum* (Schwein.) Hitchc.) bloomed during the first week in July and produced flowering heads at a height of 24 to 36 inches. Meadow grasses grew poorly during the midsummer but activity was again resumed late in August and throughout September. The tall-grass dominants, which included Indian grass, big bluestem, and switchgrass, flowered and seeded during the fall.

Grasses of secondary importance occurring in well developed tall-grass communities were *Agropyron pauciflorum*, *Phleum pratense*, *Muhlenbergia filiformis* (Thurb.) Rydb., *M. foliosa* (Roem. and Schult.)

Trin., and *Sphenopholis obtusata* (Michx.) Scribn. Grasses of secondary importance which grew chiefly on the upper edge of the zone where vegetation was commonly in phases of disturbance were *Poa pratensis* L., *P. compressa* L., *P. arida* Vasey, *Agropyron smithii*, *Agrostis exarata* Trin., *Bromus inermis* Leyss., *Panicum scribnerianum* Nash, *Hordeum jubatum*, *Agrostis hyemalis* (Walt.) B. S. P., *Distichlis stricta*, and *Elymus canadensis* L.

In 1938 few forbs were present in well developed meadows at Dewey Lake. Ten vernal, 1 estival, and 10 autumnal species were recorded, however, in areas disturbed by making hay, grazing, or by burrowing animals. Prevernal herbs were absent from the tall-grass meadow.

TRUE-RAIRIE ZONE

Communities characteristic of the true prairie dominate the upper portions of the wet meadows and form a narrow zone of transition between the mesophytic, tall-grass communities at slightly lower levels and the less mesophytic, tall grasses on the dunes. True-prairie species also invade mesic sand-dune habitats and grow in disturbed phases of the tall-grass meadows. This community is a westward extension of the true prairie, and only the most xerophytic species of that association are present. They are readily disturbed by drought and fluctuation of the water table. Clumps of grasses are often widely spaced, and true-prairie forbs occupy the interstices. This community is usually confined to a zone where the minimum depth of the water table is between 4.5 and 6.5 feet.

Canadian wild rye (*Elymus canadensis*), switchgrass, prairie dropseed (*Sporobolus asper* (Michx.) Kunth.), little bluestem, June grass (*Koeleria cristata* (L.) Pers.), and western wheatgrass were the grasses of primary importance in this zone. They are listed in the order of their ability to grow in increasingly xerophytic situations, the most xerie last.

Canadian wild rye grows in isolated clumps in the wet meadows, and it sometimes forms communities along the lower edge of the true prairie. It is also an early invader on stabilized dune sands, but it is unable to compete with the dominants either on the dunes or in the meadows. Its ecological habit is comparable to that of switchgrass, but it is less abundant because vegetative propagation is less efficient. Wild rye began growth late in April, flowered in middle July, and matured seeds in August. Production of forage was high in the wild-rye community.

Switchgrass has green leaves in the wet meadows, but a glaucous form is common as a pioneer in dry meadows and on the dunes where competition with the less mesophytic grasses is not severe. In much disturbed areas of the true prairie it had rhizomes 3 to 6 inches long and formed open bunches a few square feet in area. It attained a height of 3 to 4 feet in the most favorable habitats, but usually was not more than 2 feet high. Like slough grass, it was unable to compete with well established stands of Indian grass and big bluestem in the meadow.

Little bluestem was once a dominant in the sand hills, but since the great drought it is limited to the most favorable dune habitats. Development of tall-grass communities on the dunes under grazing as well as the occurrence of drought are the major reasons for its disappearance in recent years. Little bluestem also grows in the upper edge of the wet meadow, in areas receiving runoff water on the hard-lands, and in the rough, stony lands in river valleys. It has a compact bunch habit, begins growth in early May, and flowers in August. No inflorescences developed in dune habitats in 1937, but in 1938 many bunches revived and flowered. No seeds developed, however. Fifty bunches were observed on a south-facing dune at Dewey Lake in 1937. Twenty-two percent of them were dead, 70 percent were partially killed, and only 8 percent suffered no loss.

June grass grows in bunches and is about 16 inches tall in fruit. It begins growth in late April and flowers about the first week in June. It is therefore more successful as a pioneer on dune sands and as a dominant in the upper zones of the wet meadows than is little bluestem. Seed production during the period of study was very low. The root system is represented in Figure 22. The fine roots penetrated to a depth of 2 feet in dune sand, but did not spread laterally as is characteristic of the dominant dune bunch grasses such as sand dropseed, hairy grama, and sand-hill lovegrass (Figs. 20, 25).

Other grasses and grass-like plants found in this upper zone are the dominants and minor species of the tall-grass community already listed. The dominants of the dunes are here at the lower limits of their distribution.

Four rhizomatous perennial forbs, prairie sage (*Artemisia gnaphalodes* Nutt.), perennial ragweed (*Ambrosia coronopifolia*), smooth goldenrod (*Solidago glaberrima* Martens), and upland sunflower (*Helianthus rigidus* (Cass.) Desf.), are of primary importance in the true-prairie zone (Fig. 14). Prairie sage has the widest distribution.



FIG. 14. Smooth goldenrod (*Solidago glaberrima*) and prairie sage (*Artemisia gnaphalodes*) are common plants in true prairie and disturbed phases of the wet meadows in sand-hill valleys.

Twenty-five species of perennial and annual forbs are of secondary importance. The most common of the perennials include *Lepachys columnifera* (Nutt.) Rydb., *Potentilla arguta* Pursh, *Glycyrrhiza lepidota* Nutt., *Erigeron ramosus* (Walt.) B. S. P., *Psoralea argophylla* Pursh, *Amorpha canescens* Pursh, *Delphinium virescens* Nutt., *Tragopogon officinale* L., *Apocynum cordigerum* Greene, *Liatris squarrosa* Willd., *Tradescantia occidentalis* (Britton) Smyth., *Cirsium plattense* (Rydb.) Cockerell, *Solidago rigida* L., *Equisetum kansanum* J. H. Schaffner, *Lithospermum linearifolium* Goldie, *Verbena stricta* Vent., and *Pentstemon gracilis* Nutt. The annual and biennial forbs and grasses include *Festuca octoflora* Walt., *Helianthus petiolaris*, *Erigeron annuus* Nutt., *Sisymbrium altissimum* L., *Acmispon americanus* (Nutt.) Rydb., and *Ambrosia elatior* L.

The rhizome habit is well developed in the wet-meadow communities and is especially evident in disturbed phases of vegetation. In the lower portions of the meadow five out of nine grasses and grass-like plants propagate by rhizomes. Only little bluestem, big bluestem, and June grass grow in dense bunches. These species are at a disadvantage in areas disturbed by drought or by rapid fluctuations of the water table, grazing, or making of hay. They occur chiefly in the stable habitats where vegetation attains maximum development.

More than a third of the forbs in the wet meadows possess rhizomes. They are especially common among the composites. Species without rhizomes or with single stems are of secondary importance throughout the wet meadows, although they constituted 61 percent of the total list of forbs.

The relation of roots of several plants of the true-prairie to levels of the water table in late fall are shown in Figure 15. Here minimum water levels are too far beneath the surface for plant roots to penetrate the moist soil to the capillary fringe, a zone of moist sand 24 to 26 inches above the water table. It is probable, however, that water levels three feet above the minimum annual levels supply plants with moisture until the middle of July. After that time the water table lowers more rapidly than the roots elongate.

Changes occurred from 1936 to 1939 throughout the meadow at Dewey Lake as a result of drought and depletion of the ground water. There was, however, no disturbance from hay making. Tall grasses spread into the bluejoint-sedge zone; slough grass spread 30 to 40 feet to the upper edge of the swamp. Strong flowering culms attained a height of 6 to 8 feet (Fig. 16). Indian grass and switchgrass spread into the bluejoint-sedge zone along its upper edge. Sartwell's sedge, redtop, and smartweed spread in the upper edge of the swamp.

Data from permanent quadrats in the middle portions of the meadow revealed that Indian grass was the sole dominant in 1937, and only a few stems of big bluestem, forbs, and secondary grasses were present. The meadow was not cut during the three succeeding years. By 1939 the quadrats were domi-

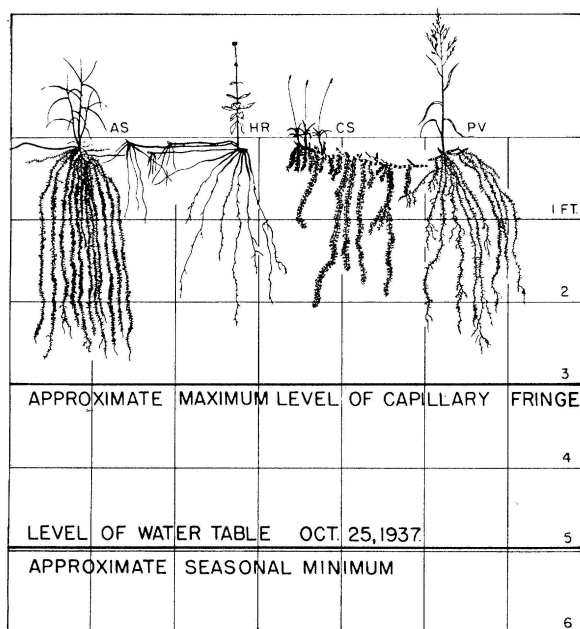


FIG. 15. Bisection showing roots of several true-prairie grasses and forbs in relation to the water table in the upper portions of the meadow at Dewey Lake in the dry year of 1937. Western wheatgrass (*Agropyron smithii*) (AS), prairie sunflower (*Helianthus rigidus*) (HR), *Carex siccata* (CS), and switchgrass (*Panicum virgatum*) (PV).

nated by big bluestem. Indian grass, timothy, and several minor grasses and forbs almost completely disappeared.

Adjustments also took place in the upper meadow. General observation revealed that the sand-dune grasses slowly increased at the expense of forbs from 1936 and 1939.

Several changes result from grazing and hay making. Prairie sage and many of the less common forbs are grazed by cattle, but perennial ragweed, blue vervain (*Verbena stricta*), ironweed (*Vernonia*



FIG. 16. Bluejoint (*Calamagrostis canadensis*) and sedge (*Carex* sp.) community invaded during the summer of 1937 by slough grass (*Spartina pectinata*), the tall grass in the background, as a result of rapid lowering of the water table.

fasciculata Michx.), and narrowleaved goldenrod (*Euthamia camporum* Greene) are not palatable and therefore increase in heavily grazed pastures. Bee-weed (*Peritoma serrulatum* (Pursh) DC.) is an odorous, annual plant which grows in large numbers in similar situations. *Eragrostis spectabilis* (Pursh) Steud. grows in bunches 10 to 16 inches in height and forms conspicuous stands on the upper edges of meadows, being especially conspicuous in September. This grass, however, occurs mainly in areas disturbed by hay making.

TALL GRASSES ON THE DUNES

Tall grasses characteristic of sand habitats occur on the dunes and form broad ecotones with the mixed prairie of the hardlands and with the true prairie on the upper edge of wet meadows. The several sand-hill dominants are distributed in communities according to variations in aerial environment and in efficiency of infiltration of rain by the various textures of sand. They are all postclimax species. The efficiency of sand in absorbing rainfall without loss by runoff and in almost entirely preventing evaporation from its surface provides the compensating factor. This factor is especially important during summer when rainfall is limited and evaporation is high. The several communities of dune grasses vary in composition and in structural characteristics such as density of vegetation, seasonal aspects, and layering. The line of demarcation between these communities of dune grasses and the mixed prairie is somewhat indefinite, but boundary lines between them and true prairie are narrow and well defined.

SUCCESION AND DEGENERATION

The *Redfieldia flexuosa* community represents the earliest phases of development of sand-hill vegetation; communities of *Muhlenbergia pungens* follow somewhat later in succession. Several well developed communities in dune-sand and hardland habitats are found mainly on the Fort Niobrara Game Preserve where vegetation has been free of grazing for a long period of time. Certain winter pastures, however, have a similar composition because they are not disturbed during the growing season. Sand-hill bluestem, sand-hill lovegrass, and sand reedgrass are the main components of the fully developed communities on dune sands. Hairy grama, sand dropseed, and sand-hill sedge (*Carex heliophila* Mackenzie) are important species in the ground layer.

Species of secondary importance on dune sands are little bluestem, June grass, switchgrass, *Cyperus schweinitzii* Torr., Indian ricegrass (*Oryzopsis hymenoides* (Roem. & Schult.) Ricker), and porcupine grass (*Stipa spartea* Trin.). Mixed-prairie grasses which invade dune sands along the zone of contact in order of decreased importance are western needlegrass, blue grama, and western wheatgrass.

Most of the palatable species have been selectively grazed on most of the ranges for so long a time that they are not as numerous as the less palatable

ones. The palatable species are sand-hill lovegrass, sand-hill bluestem, and switchgrass. The growth of sand reedgrass as well as hairy grama and sand-hill sedge is also reduced by grazing. The species which are less palatable or which respond quickly to increased moisture supply in disturbed communities become the dominants in disclimax communities. Sand reedgrass and sand dropseed are the most important species. On severely degenerated ranges, *Muhlenbergia* is the chief grass because it is not readily grazed. Degeneration of a sand-hill range thus falls into three stages; decrease of the most palatable species, dominance of *Calamovilfa* and sand dropseed, and finally dominance of *Muhlenbergia*. This is approximately the inverse order of development of vegetation.

Redfieldia flexuosa.—Since the stabilization of sand-hill habitats by control of fire and development of vegetation under grazing, the areas suited to blowout grass have been materially reduced. Blowout grass is a tall mesophytic species which grows on both the leeward and windward sides of blowouts and occasionally in severely disturbed phases of sand-hill vegetation (Fig. 17). It spreads by long,



FIG. 17. A general view of a community of blowout grass (*Redfieldia flexuosa*) on the leeward side of a blowout southwest of Valentine.

slender rhizomes which are 6 to 24 inches deep. The long, flexuous culms and leaves grow 20 to 36 inches tall. Roots occur at the nodes of the rhizomes and penetrate to a depth of 4 feet. There are numerous laterals 0.5 to 2 inches in length (Fig. 18).

Redfieldia grows most actively near the bottoms of blowouts where wind erosion is reduced. The aerial environment in the blowouts is characterized by strong winds, high temperatures, and bright light, but moisture is available throughout most of the growing season, and competition for moisture is almost nil. Long, slender rhizomes spread into the unstabilized portions of the blowouts in summer, but these are exposed in winter when wind erosion is most active. Initiation of stabilization is not the result of revegetation and is possible only when the blowout has developed a streamlined, mature form.

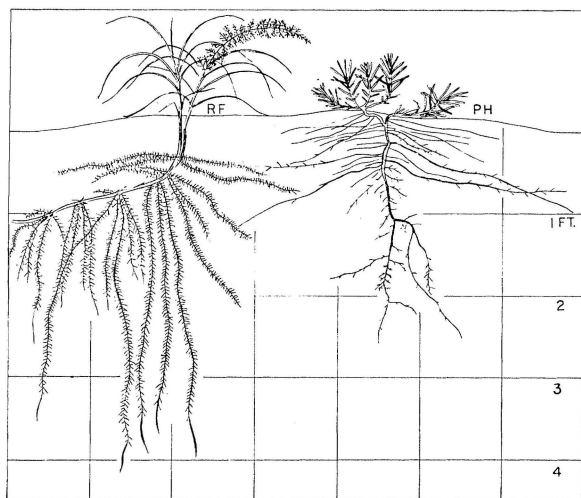


FIG. 18. Bisect showing characteristic root systems of *Redfieldia flexuosa* (RF) and *Pentstemon haydeni* (PH) in a blowout near Valentine.

This pioneer community of *Redfieldia* is readily displaced by more xerophytic grasses such as *Muhlenbergia*.

A summary of stem counts of grasses in 25 quadrats from 5 separate *Redfieldia* stations is shown in Table 2. *Redfieldia* maintained an open growth in

TABLE 2. A summary of the total number of bunches (number in parenthesis) or stems of grasses from 10 census and basal area quadrats from each of 10 stations in several phases of development of the *Redfieldia* and *Muhlenbergia* communities. The stations are listed in order of increased complexity from left to right.

	Redfieldia communities					Muhlenbergia communities				
<i>Redfieldia flexuosa</i>	276	812	587	714	608	140	5	27
<i>Muhlenbergia pungens</i>				71	...	190	1354	3302	902	1026
<i>Andropogon hallii</i>						81	15	2	16	44
<i>Calamovilfa longifolia</i>							41	26	163	86
<i>Sporobolus cryptandrus</i>							8	18	16	16
<i>Bouteloua hirsuta</i>							(1)	(4)	(33)	(126)
<i>Cyperus schweinitzii</i>							3	...	7	14
<i>Carex heliophila</i>								8	10	6
<i>Stipa comata</i>								(2)
<i>Koeleria cristata</i>								(14)	(4)	(3)
<i>Aristida longiseta</i>									3	...
<i>Andropogon scoparius</i>									(4)	(31)
<i>Eragrostis trichodes</i>									(1)	...
Total basal cover in sq. cm.	130	400	255	390	308	344	1424	1810	914	2631

the first stages of development, but as succession proceeded both the number of stems and number of species increased. Perennial forbs were *Rumex venosus* Pursh, *Pentstemon haydeni* S. Wats., *Comandra pallida* A. DC., *Phaca longifolia* (Pursh) Nutt., *Oenothera albicaulis* Pursh, *Lygodesmia juncea*

(Pursh) D. Don., and *Petalostemon villosus* Nutt. Sixteen species of annuals were also found. These were widely spaced, and those which maintained short, prostrate growth were the most numerous. With the exception of *Rumex venosus*, *Pentstemon haydeni*, *Oenothera albicaulis*, and *Phaca longifolia*, all the forbs persisted in the *Muhlenbergia* stage of development, but only *Psoralea* and *Lygodesmia* were found in the well developed dune communities. Many of the annual forbs also occurred only in the *Redfieldia* community. Basal cover from 25 quadrats averaged about 0.5 percent of the total area. *Redfieldia* is not readily grazed during the growing season, but since it remains green for a time after other dune grasses have become tough and dry, it is utilized by cattle in the fall.

Muhlenbergia pungens.—Sand-hill muhley is a pioneer on relatively stable dune sands and acts as a successor to *Redfieldia* because of its more compact growth and efficient root system (Fig. 19). Pioneer



FIG. 19. Sand-hill muhley (*Muhlenbergia pungens*) growing on dune sand. (Photograph by J. E. Weaver.)

colonies of sand-hill muhley often completely cover areas of a few to several square feet. These catch the blowing sands and further stabilize the habitat. The pioneer bunches grow most luxuriantly. As the dominant grasses increase, sand-hill muhley is weakened and disappears entirely from the tall-grass communities. It becomes a permanent part of sand-hill vegetation only on tops of dunes where absorption of rain is at a maximum, but where aerial environment is more severe than in any other dune habitat.

The leafy, prostrate, rhizomatous culms are 4 to 6 inches in length, and 3 to 4 are produced each spring from the perennial portions of the culms of the preceding year. Vigorous plants develop one to six new roots per stolon each year during early June. In weak plants, new growth depends upon roots already established. The roots of primary rank attain a length of 3 to 4 feet, but the laterals are not numerous and are widely spaced (Fig. 20). The roots, which approximate a millimeter in thickness, are unable to deplete soil moisture rapidly.

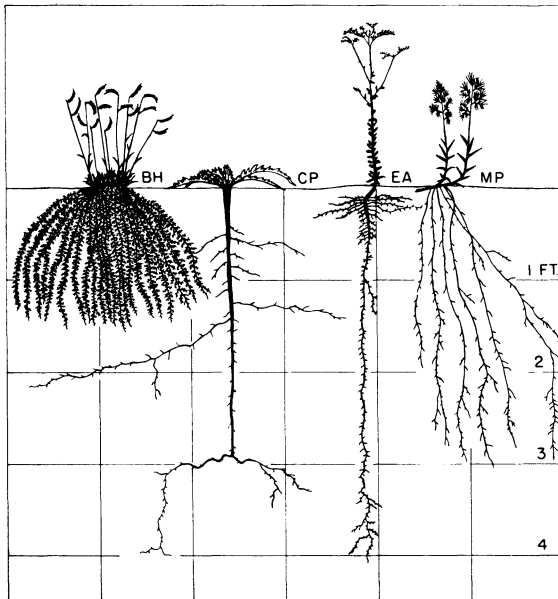


FIG. 20. Bisect on top of dune showing general form of root systems of several species in the sand-hill muhley-hairy grama community. *Bouteloua hirsuta* (BH), *Cirsiium plattensis* (CP), *Eriogonum annuum* (EA), and *Muhlenbergia pungens* (MP).

The glaucous, stiff leaf-blades are from 1 to 2 inches in length and 9 to 13 are usually present per culm. They are not readily grazed, and consequently the grass thrives in areas disturbed by grazing. Reddish inflorescences, 10 to 14 inches in height, are produced throughout the summer whenever there is a sufficient water supply. Where competition is not great, production of seed is abundant.

The several *Muhlenbergia* communities are arranged in order of increased complexity in Table 2. The first four stations were on the Valentine Lakes Refuge where grazing had kept dune vegetation in early phases of development. The fifth was on the Fort Niobrara Game Preserve where the dunes had not been disturbed by grazing since 1914. Early development of the community is characterized by an increase in number of species of grasses and forbs as well as in number of plants. Late development is indicated by the disappearance or decrease of pioneer perennial grasses and forbs and nearly all of the annual species. The dominant grasses increase. These changes are caused largely by competition for moisture. Basal cover also increased with maturity of the community. In an early phase of development it averaged 82 square centimeters per quadrat, but in a final phase, 526, an increase of 540 percent. Basal cover, as a result of the bunch habit and prostrate growth of the dominants, was 2.7 percent higher than in any other dune community.

Andropogon hallii.—Sand-hill bluestem is a tall grass which is a common pioneer in blowouts. As a pioneer it is exceeded only by Redfieldia and *Muhlenbergia*. Mature communities occur in somewhat more

mesophytic dune habitats than either the mature stands of sand-hill muhley and hairy grama on top of the dunes or those of *Calamovilfa* on the lower portions of the south slopes. This is a habitat where the winds are ameliorated somewhat by topography and where the sand texture is coarser than that at lower portions of the dune. Mature *Andropogon* communities also are found on the tops of low, rolling dunes or in local areas of coarse sand.

Calamovilfa is a common codominant, but it attains neither the height nor density of sand-hill bluestem. Hairy grama is the most important species in the ground layer. It produced twice as much forage as the sand-hill sedge, sand dropseed, little bluestem, and June grass, the other members of the ground layer. *Muhlenbergia* and two mixed-prairie species, western needlegrass and blue grama, occurred in small quantities. The *Andropogon* community had 20 percent less basal cover than that of sand-hill muhley. The leaves of sand-hill bluestem are readily grazed by cattle, and therefore this species is not common on the heavily grazed ranges.

Sand-hill bluestem grew 3 to 5 feet tall and had 6 to 9 glaucous, tender leaves per culm. The blades approximated 1 centimeter in maximum width and often attained a length of 14 to 16 inches. Growth began early in May, and flowering took place from the first week in July until September, according to the occurrence of rain. Seeds were seldom formed in well developed communities.

Sand-hill bluestem maintained an open growth in the mature communities, but in the blowouts it formed dense branches. In the former, the rhizomes were 4 to 8 inches in length, but in the blowouts they did not exceed 4 inches. This is an adjustment to differences in competition for water. Rhizomes made their greatest growth in spring, and roots originating from the nodes late in May penetrated to depths of 4 to 6 feet. An average of 14 roots per rhizome was found on well developed plants by August, 1938.

Eragrostis trichodes.—Sand-hill lovegrass grows on north slopes of dunes where it is protected from desiccating south winds (Fig. 21). The most mesic and most extensive communities are found on the highest dunes. It forms a narrow ecotone with the *Calamovilfa* community near the bottom of the dunes, and on the upper portions it is mixed with *Andropogon* and *Muhlenbergia*. Since it is highly palatable the stand cannot be maintained under summer grazing. Lovegrass is slow to invade blowouts, but easily supplants *Muhlenbergia* and hairy grama once invasion begins.

Sand-hill lovegrass grows in widely spaced bunches. At Fort Niobrara where an average of 7 bunches were present in each quadrat, the average basal cover per bunch from 25 quadrats was 25 square centimeters. At Valentine Lakes Refuge the average from 12 quadrats was 21.7 square centimeters. The reddish-green blades were about 1 cm. in width and rolled tightly during periods of drought. Five to seven leaves 8 to 16 inches in length were present on each culm, and the inflorescences, under favorable condi-

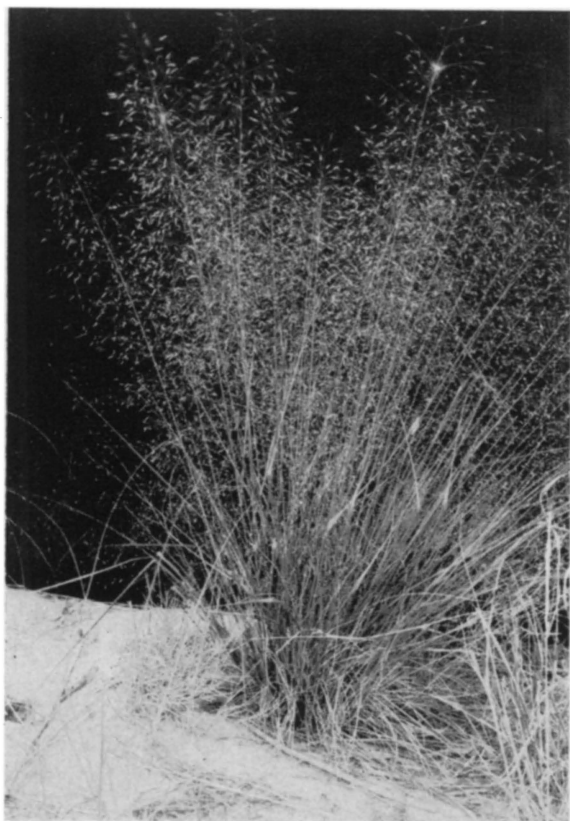


FIG. 21. Sand-hill lovegrass (*Eragrostis trichodes*) in open dune-sand area showing its bunch habit and flowering culms.

tions, attained a height of 30 to 40 inches. An abundance of seed developed at Valentine Lakes Refuge after the fall rains of 1937 and 1938.

The roots did not penetrate beyond a depth of 18 inches, but spread 18 to 30 inches laterally (Fig. 22). An average of 13 roots originated from each new

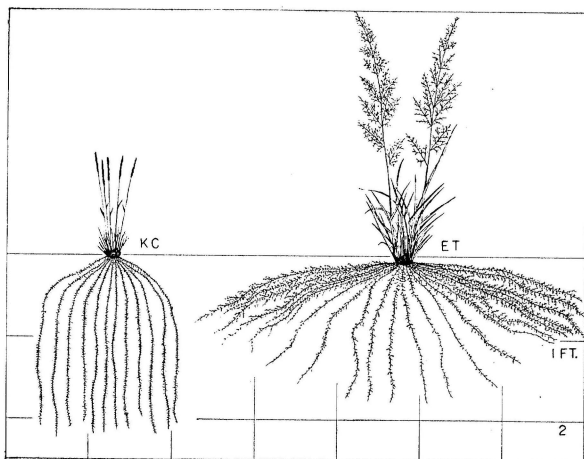


FIG. 22. Bisect showing general form of root systems of June grass (*Koeleria cristata*) (KC) and sand-hill lovegrass (*Eragrostis trichodes*) (ET) on north-facing side of dune at Fort Niobrara.

rhizome in 1938. The small roots are numerous and thoroughly spread through the surface sands.

The well developed community of lovegrass excludes both the short bunch grasses and the tall grasses. In the disturbed community, however, the tall grasses of dunes and the short bunch grasses were dominant. Three bunch grasses (lovegrass, western needlegrass, and little bluestem) had only 9.3 percent of the basal cover they occupied in the climax community, but in the disclimax community hairy grama and June grass had 446 percent more bunches. The dune tall grasses (sand reedgrass, sand-hill bluestem, and switchgrass) had 60.5 percent more culms.

Calamovilfa longifolia.—Sand reedgrass is the most characteristic grass of the sand hills. It grows in a wide range of habitats from the coarsest dune sand to the very fine sandy loams, but it makes its best growth on the south slopes of dunes and the broad, dry valleys (Fig. 23). Codominants vary according to sand texture and the degree of grazing. Hairy grama, blue grama, and western needlegrass are the major codominants in well developed communities, but on dunes sand dropseed is the major one in disturbed phases caused by grazing, and on fine sands, especially in the dry meadows, blue grama is the major codominant under grazing.



FIG. 23. Sand reedgrass (*Calamovilfa longifolia*) on the left and sand dropseed (*Sporobolus cryptandrus*) on the right on Valentine sand in a dry meadow at Dewey Lake.

Calamovilfa attains a height of 30 to 40 inches. The best developed culms had 10 to 12 glaucous, fibrous leaves with blades 15 to 20 inches long and nearly a centimeter wide. The leaves roll readily when moisture is not available. They withstand long periods of drought, but quickly revive upon receiving moisture. Development began late in April or early in May, and much growth was made during spring. Flowering occurred from July to September, but formation of seed was usually confined to plants growing in disturbed areas where moisture was more abundant.

Sand reedgrass propagates almost entirely by rhizomes. One to five new rhizomes per culm developed in May and June. They varied in length from 3 to 10 inches, and remained dormant until the following spring when a single culm and several new roots developed from each rhizome. A few roots, however, developed shortly after the rhizomes began to grow. Rhizomes excavated August 18 had an average of 13 roots each. These roots were nearly 4 feet long and 2 to 3 mm. in diameter, except at the starch-laden tips where they were sometimes 10 mm. in thickness (Fig. 24).

In pure stands of *Calamovilfa*, basal cover was low, with a total of only 1 percent, but where the bunch grasses were present it was greater. Where it accompanied sand reedgrass and hairy grama, basal cover was 2.5 percent, but where it occurred with blue grama a cover of 1.9 percent was found. Where sand reedgrass was codominant with needlegrass, the cover was 4.4 percent.

The sand reedgrass-hairy grama community grows on the tops of broad, low dunes where movement of wind is not as great as on the tops of high ones. The ground layer of bunch grasses comprised 27 percent of total plant units (that is, stems or bunches) and 89 percent of the basal cover.

The sand reedgrass-blue grama community (Table 2) represents a transition toward the hardlands where neither the short-grass nor the tall-grass dominants made their best growth. Here, however, *Calamovilfa* was most important. It comprised 25.6 percent of the basal cover but occupied only 1.9 percent of the area. Among the grasses of secondary importance, sand dropseed and sand-hill bluestem ranked second and third in basal cover. Sand-hill sedge and blue grama formed a ground layer beneath the tall grasses.

In ungrazed areas on Fort Niobrara Game Preserve the *Calamovilfa longifolia-Stipa comata* community occurs on the harder portions of the sand hills, especially in the Valentine soil areas where hygroscopic coefficients are 3.0 to 3.5 percent. Sand reedgrass and needlegrass completely excluded blue grama, and sand dropseed occupied a place of secondary importance. Basal cover was 4.8 percent. Needlegrass composed 64 percent of total basal cover and was followed in importance by sand dropseed, sand reedgrass, and sand-hill lovegrass in the order named.

Sporobolus cryptandrus.—Sand dropseed is a pioneer in abandoned fields of fine sandy loams and grows in small quantities in disturbed phases of the mixed prairie, but it does best on sand-hill range where it is codominant with sand reedgrass (Fig. 23). It maintains itself in climax vegetation as a dominant only in a zone of transition where thin layers of sand overlies fine sandy loams, and is present in small quantities throughout the well developed sand-dune communities.

Sand dropseed has an open bunch habit. The culms attained a height of 3 feet under favorable conditions of moisture during late August or early September, but with a smaller water supply the height was only 1.5 to 2 feet. Growth began in late April or early May. By the middle of May 1938, 3 or 4 green leaves were present per culm, and on August 30, an average of 9 was recorded on well developed plants. The leaf blade was 7 to 8 inches in length. At Fort Niobrara in 1938 and 1939, flowering took place during the first two weeks of September, but in 1937, during the last week of August. The inflorescences elongated beyond the sheath under conditions favorable to growth. An abundance of seed developed every year. It is by prolific seeding that this species is able to maintain itself as a pioneer and as a disclimax species.

Sand dropseed has a shallow root system which utilizes light summer rains effectively (Fig. 25). The main roots were a millimeter in diameter, attained an average length of 18 to 24 inches, and had a maximum length of 36 inches in the blue grama-sand dropseed community. These with their fine branches thoroughly occupied the surface foot of sand in 1938. The number varied from 3 to 10 according to the vigor of the individual plant.

Carex heliophila.—Sand-hill sedge is common in well developed vegetation where it attains a height of 3 to 6 inches. About 16 plants per quadrat were present in the sand-hill bluestem community; 17 in the sand reedgrass community; and 19 in the community dominated by sand reedgrass and blue grama. This sedge is less conspicuous on the top and north slopes of dunes and is seldom found in the mixed prairie, where it is regularly replaced by *Carex filifolia*. It is not abundant on range land. An open growth results from development of stolons 4 to 8 inches long. Fine roots penetrate into the sand 8 to 16 inches. Growth begins early in April, and seeds mature by the first week in June. It is semidormant during summer but revives in the fall when moisture is present and temperatures moderately low.

FORBS ON SAND DUNES

Forty-eight perennial forbs were recorded on the sand dunes, but only five were of much importance. In addition, 3 biennials, 19 annuals, 3 cacti, and 6 half-shrubs were present. The average number of forbs from 25 quadrats in well developed sand-dune communities was 8. The sand-hill muhley-hairy grama community had about 19 forbs per

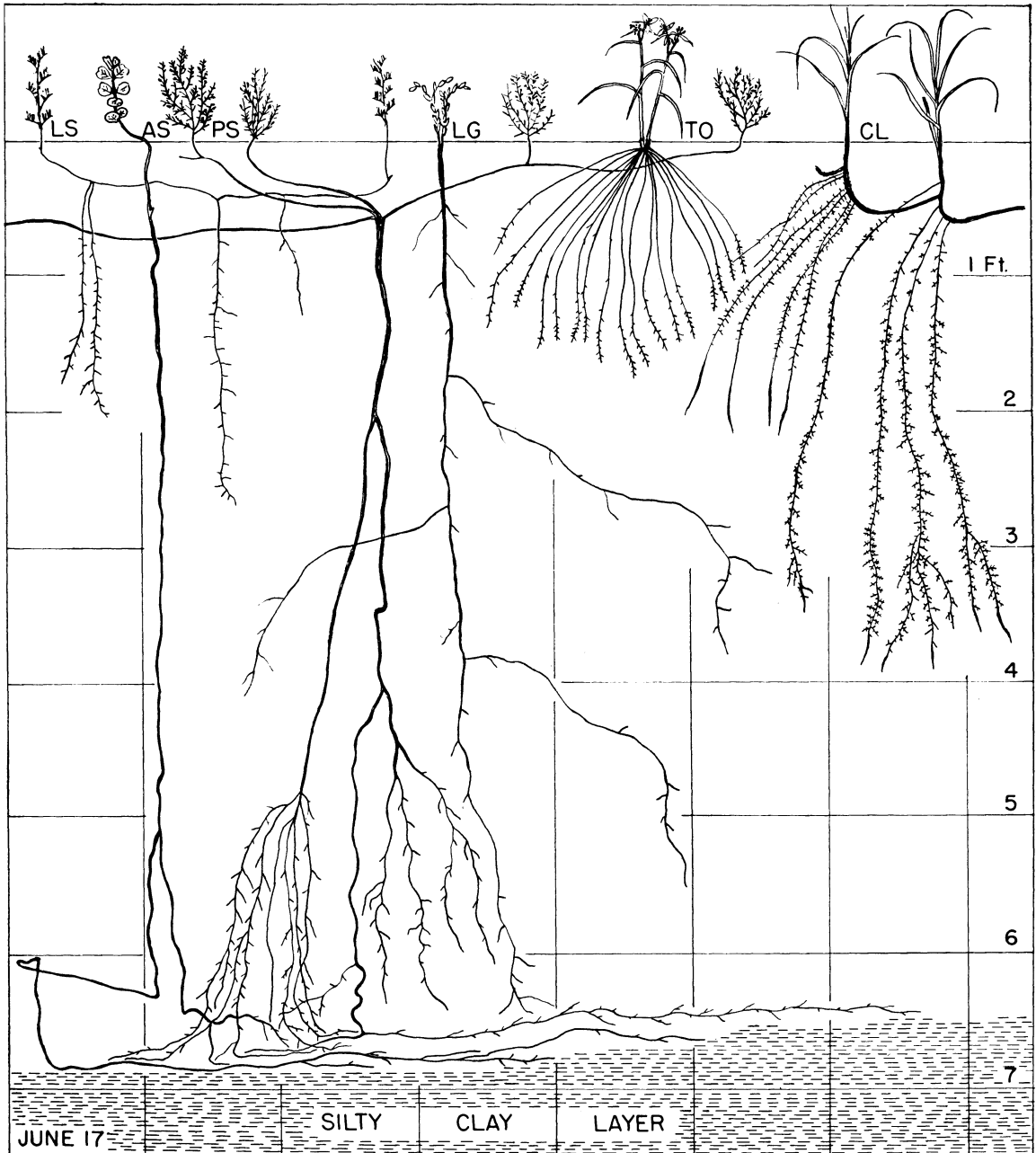


FIG. 24. Bisect showing general form of root systems of several typical sand-dune forbs and grasses growing in sand. *Lathyrus stipulaceus* (LS), *Asclepias arenaria* (AS), *Psoralea lanceolata* (PS), *Lithospermum gmelini* (LG), *Tradescantia occidentalis* (TO), and *Calamovilfa longifolia* (CL).

quadrat, and the sand reedgrass-blue grama community only 3. The number of species of forbs was four times as great as that of grasses, but the basal area of forbs composed only 15.6 percent of the total cover.

The forb populations increased when the dominant grasses were disturbed by grazing or other denuding agents. Communities which were subjected to dis-

turbances over a long period of time had numerous perennial forbs and shrubs, but there were many annual forbs in areas which were disturbed for only a short time.

The forbs and shrubs varied greatly as to their ecological habits and characteristics. Certain species were distinctly pioneers which could not withstand competition. Some were able to endure competition

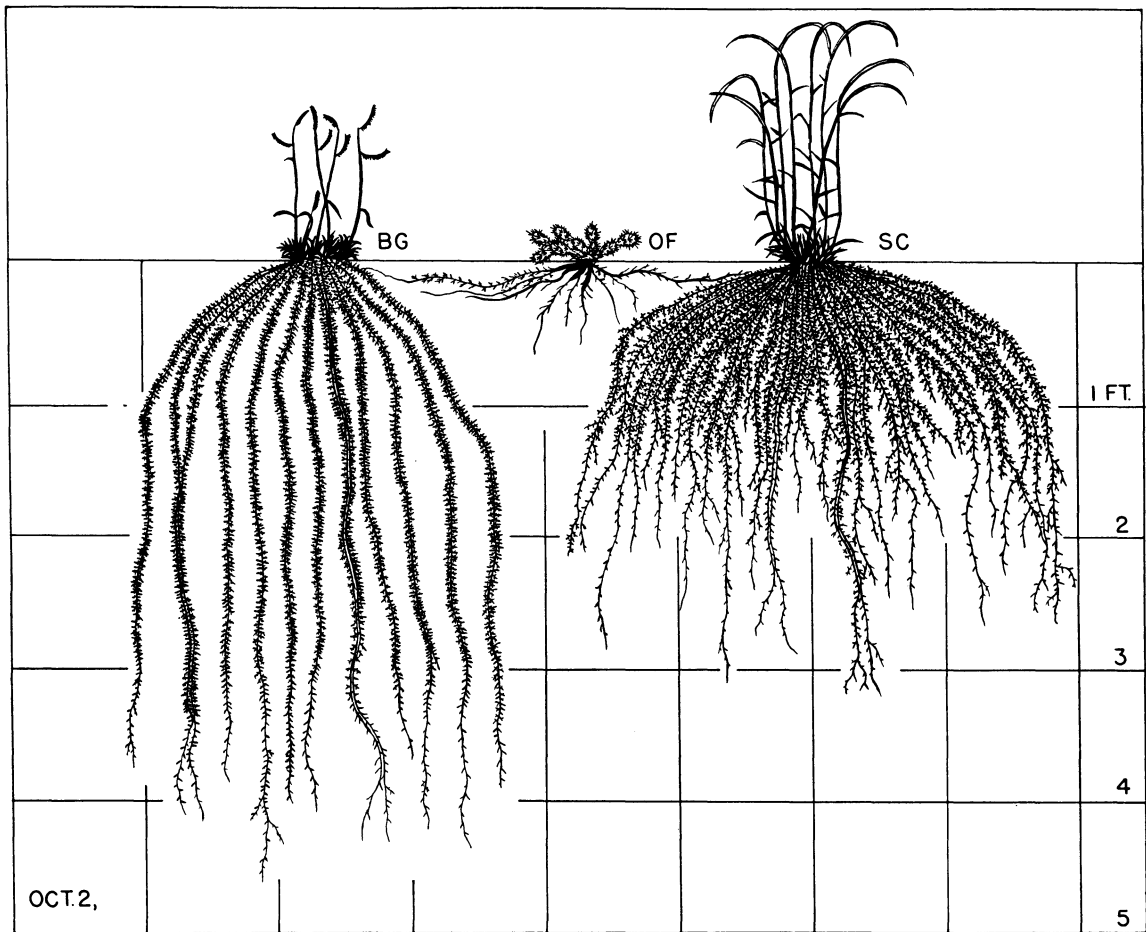


FIG. 25. Bisect showing characteristic root habit of sand dropseed (SC), blue grama (BG), and *Opuntia fragilis* (OF) in the sand dropseed—blue grama community.

with the dune grasses, and others were drought evaders which matured in spring and soon died. Thus the forbs may be placed in various groups.

The five major perennial forbs are spiderwort (*Tradescantia occidentalis*), skeleton weed (*Lygodesmia juncea*), prairie sage, perennial ragweed, and sand psoralea (*Psoralea lanceolata*). Spiderwort frequently grows where competition with the dune grasses is severe, but its growth is aided by disturbance. It is readily grazed by cattle during spring and therefore does not occur abundantly on range lands, but is common in upland pastures used primarily for winter range and for hay making. It flowers in June, seeds immediately, and becomes dormant during the first summer drought. It renews growth in the fall, however, if moisture is present. Migration is by seed only. The succulent roots, which are about 2 mm. in diameter, have only a few laterals and penetrate into the sand 16 to 20 inches (Fig. 24). Spiderwort may be classified as a drought evader.

Skeleton weed is characterized by long slender stems and branches which have leaves only in a rudi-

mentary form. It propagates by long rhizomes. Some flowering heads develop after summer rains, but few seeds mature. Skeleton weed grows on both the sand dunes and the hardlands. Since the stems are grazed by cattle, few plants are found in overgrazed pastures.

Sand psoralea forms socias on dunes and in dry meadows in well developed vegetation, but it makes its best growth as a pioneer in blowouts or in other disturbed places. It spreads by rhizomes from a central root which penetrates to a depth of 8 to 10 feet (Fig. 24). The leaves and pods have an offensive odor and are not readily grazed. The plants remain green throughout the summer in blowouts where they do not compete with grasses, but in mature communities this legume produced no seed and dried soon after the first drought.

Both perennial ragweed and prairie sage spread by rhizomes and thus form large socias. Their root systems are shallow and, therefore, the plants must withstand long summer drought. On receiving moisture, however, they quickly revive. The ragweed is less palatable than the sage and therefore persists

under heavy grazing. Both flower in late summer or fall.

A group of unpalatable, perennial forbs grow where the grasses have been weakened or destroyed by grazing and are thus valuable as indicators of disturbance. Riddell's groundsel (*Senecio riddellii* T. & G.) is a poisonous weed bearing yellow flowering heads in September at the top of stiff stems with narrowly pinnate, succulent leaves. A taproot penetrates 4 to 5 feet beneath the surface.

The bush morning glory (*Ipomoea leptophylla* Torr.) attains a height of 2 to 3 feet; the stems spread 3 to 4 feet laterally from a central crown. The plant is characterized by a fleshy, deep taproot in which water accumulates during periods of rain. Purple flowers appear in the middle of July.

Solitary plants of sand stoneseed (*Lithospermum gmelini* (Michx.) Hitchc.) are scattered throughout the dune habitats. Orange flowers appear in early June. The black taproot penetrates to a depth of 6 to 7 feet (Fig. 24).

The Platte thistle (*Cirsium plattensis*) has a taproot which penetrates to a depth of 3 to 4 feet (Fig. 26). Cream-colored heads appear late in May or early in June.

Certain pioneer plants are unable to withstand competition with the xerophytic grasses. Chief among these are *Rumex venosus*, *Pentstemon haydeni*, *Oeno-*

thera albicaulis, *Phaca longifolia*, *Comandra pallida*, *Petalostemon villosus*, *Oenothera nuttallii* Sweet, and *Machaeranthera canescens* (Pursh) A. Gray. All but *Pentstemon*, *Petalostemon* and *Machaeranthera* are stoloniferous.

A third group, including *Equisetum kansanum*, *Physalis heterophylla* Nees., *P. virginiana* Mill., *Solidago glaberrima*, and *Helianthus rigidus*, has rhizomes, but is of secondary importance. Seldom, if ever, do these species grow in blowouts, but they invade stabilized sands denuded of vegetation, or grow in the most favorable dune environments. They are true-prairie species on the edge of their geographical or ecological range.

Twenty-four perennial species have no rhizomes and therefore are scattered over the dunes as isolated individuals. They are usually late invaders which can withstand competition with the more xerophytic of the dune grasses, but develop best where vegetation is disturbed. They possess deep taproots. The major species in this group are *Lithospermum linearifolium*, *Ipomoea leptophylla*, *Artemisia caudata* Michx., *Lithospermum gmelini*, *Liatris squarrosa*, *Petalostemon purpureus* (Vent.) Rydb., *P. oligophyllum* (Torr.) Rydb., *Hymenopappus filifolius* Hook., *Oenothera serrulata* Nutt., *Cirsium plattensis*, *Senecio riddellii*, *Psoralea digitata* Nutt., *Chrysopsis villosa* (Pursh) Nutt., *Sideranthus spinulosus* (Pursh) Sweet, *Acerates angustifolia* (Nutt.) Dec., *Asclepias arenaria* Torr., and *Kuhnia suaveolens* Fresen.

A small group of forbs persists in grasslands because of their ability to flower and seed in spring and go into dormancy during the first summer drought. These plants do not readily invade denuded areas but are benefited somewhat by disturbance of the dominant grasses. They occur in a wide range of sandy habitats. Chief among them is *Tradescantia occidentalis*, but plants of similar habit listed in order of importance are *Lathyrus stipulaceus* (Pursh) Butters and St. John, *Pentstemon angustifolius* Pursh, *Lesquerella ludoviciana* (Nutt.) S. Wats., *Senecio plattensis* Nutt., and *Towsendia* sp.

A total of 12 annual forbs and 2 annual grasses grow on disturbed dune sands where competition with the dune grasses is not great. The most common forbs are sand-hill sunflower (*Helianthus petiolaris*), sand spurge (*Euphorbia petaloidea* Engelm.), and narrow-leaved lambsquarter (*Chenopodium leptophyllum* Nutt.). The following annual plants are unable to withstand competition with dune grasses and therefore are present, but in small numbers only, in the most severely disturbed areas. Two chief annual grasses on dune sands are *Triplasis purpurea* (Walt.) Chapm. and *Cenchrus pauciflorus* Benth. The forbs include *Froelichia campestris* Small, *Euphorbia serpens* H. B. K., *Cristatella jamesii* T. & G., *Cycloma artriplicifolium* (Spreng) Coult., *Salsola pestifer*, *Corispermum villosum* Rydb., and *Lygodium rostrata* A. Gray.

Three biennial plants in sand-hill habitats are *Eriogonum annuum*, *Oenothera rhombipetala* Nutt.,



FIG. 26. Platte thistle (*Cirsium plattensis*) and leaves of sand-hill bluestem (*Andropogon hallii*) on the side of dune in early June.

and *Hymenopappus tenuifolius* Pursh. They are unable to compete with the perennial grasses and therefore indicate disturbances.

Shrubs, listed in order of their importance, include soapweed (*Yucca glauca* Nutt.), sand cherry (*Prunus besseyi* Bailey), poison ivy (*Toxicodendron radicans* (L.) Kuntze), prairie rose (*Rosa arkansana* Porter), Macoun's rose (*R. macounii* Greene), and small red-root (*Ceanothus ovatus* Desf.). They grow best on protected hillsides or in areas where grass cover is reduced by grazing, but occur in small quantities throughout all dune habitats. Sand cherry, prairie rose, and poison ivy have rhizomes, and the roots penetrate to a depth of 8 and 12 feet (Fig. 27).



FIG. 27. A typical view of a sand-hill community in which sand-hill bluestem (*Andropogon hallii*) and sand reedgrass (*Calamovilfa longifolia*) grow above bunches of hairy grama (*Bouteloua hirsuta*).

Sand cherry flowers early in May, and the others early in June. Fruits develop only during favorable seasons.

Soapweed is conspicuous on heavily grazed ranges and on rough, stony lands. It is seldom found where vegetation is well stabilized. Its stiff, long leaves remain green throughout the winter. The pods appear shortly after flowering and are eaten by cattle. According to the ranchers, the crowns of soapweed are often grazed during the winter, but the plants are not disturbed in the summer when there is an

abundance of green forage. Soapweed increased under heavy grazing.

GENERAL RELATIONS OF THE FLORA

The highly diversified and well developed vegetation of the dunes points to a great age and an early historical development of the sand-hill flora. Geological evidence reveals that sand habitats have existed in this region since early Tertiary times. Generic composition of the dune vegetation and the true prairie is similar. The dominant grasses and many of the major forbs of the two communities, however, are distinctly different in species, and some genera are entirely characteristic of sandy habitats. This indicates that the development of dune vegetation was independent of that of true prairie but contemporaneous with it.

Five dominant genera, including *Muhlenbergia*, *Bouteloua*, *Andropogon*, *Eragrostis*, and *Sporobolus*, are represented in the flora of the true prairie and the sand hills. Three of these (*Andropogon*, *Sporobolus* and *Bouteloua*) have species which are dominant in the true prairie. *Muhlenbergia* and *Eragrostis* are important in the sand-hill flora, but species of these genera are usually disclimax in the true prairie. Only three true-prairie grasses occur on the dunes. *Stipa spartea* is found occasionally; June grass and little bluestem grow only in the most favorable places.

Two genera, each with a single species, are confined to dune habitats. Of these *Calamovilfa* is the most characteristic of the sand-hill flora and *Redfieldia* is the most important pioneer in blowouts. Among the forbs there is no genus which occurs only on the dunes, but 52 percent of the species are confined to sandy habitats. Generic relations to the mixed prairie in Nebraska are found only in *Bouteloua*, but the ecological ranges of the several dune and mixed-prairie dominants overlap, causing mixtures along a broad zone of contact.

Physiologically, the sand-hill grasses are adapted to a mixed-prairie climate under which they withstand severe aerial environment and endure long periods without rain. As a result of efficient absorption of summer rains, more moisture is available to the individual plant in the sand hills than on the hardlands. Wide spacing of plants and ability of certain species (including the tall grasses) to penetrate several feet into the sand are adaptations to the habitat. They are, however, unable to withstand competition of the mesophytic tall grasses in the meadows. Conversely, they are too mesic to endure competition with the climax grasses on the hardlands.

LAYERING

Two grasses are usually dominant in dune communities, and several grasses and forbs occupy a position of secondary importance (Fig. 27). One dominant is usually a tall grass and another a short bunch grass. The major tall grasses are *Calamovilfa longifolia* and *Andropogon hallii*. To this group *Redfieldia flexuosa* may be added, though it grows

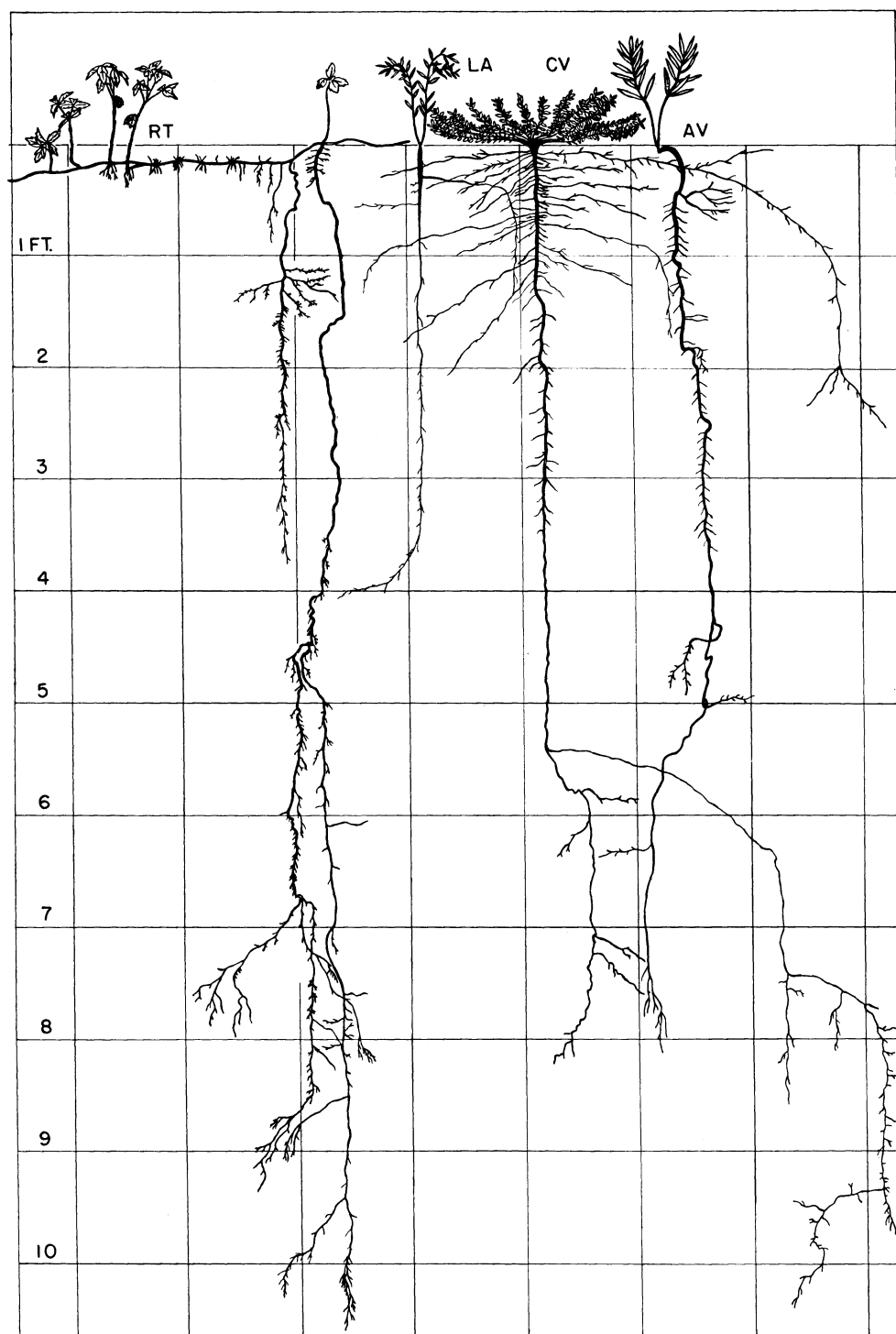


FIG. 28. Bisect showing root systems of several typical sand-dune forbs and shrubs. Poison ivy (*Toxicodendron radicans*) (RT), narrow-leaved puccoon (*Lithospermum linearifolium*) (LA), *Chrysopsis villosa* (CV), and *Acerates* sp. (AV).

only occasionally in a mixed community. Sand-hill muhley, though shorter in stature, is an ecological equivalent of the tall dune grasses. The typical tall dune grasses form a layer 2 to 4 feet above a lower stratum which is composed primarily of hairy grama, sand dropseed, sand-hill sedge, blue grama, western needlegrass, and many of the forbs. The true-prairie bunch grasses—little bluestem and June grass—are not only of secondary importance, but also attain a height only slightly greater than the short bunch grasses.

The short-grass layer is poorly developed in the *Eragrostis* community on the dunes. The tall-grass layer is absent only in the sand-hill muhley-hairy grama community on the tops of the dunes, where sand-hill muhley occupies the ecological position of a tall grass. It has a root growth similar to the tall grasses and is more mesophytic than its bunch-grass codominant. Absence of the ground layer in the *Eragrostis* community is the result of inability of the short grasses to withstand shading by the tall grasses and competition for moisture with a larger grass of similar root habits.

Layering is clearly evident beneath the soil surface just as it is above. There are two layers above ground and two below. A group of xerophytic bunch grasses are rooted only 12 to 18 inches deep, and are dependent upon summer rain for most of their water. Their fine roots thoroughly ramify the surface sands, and the plants transpire all available water soon after a rain. Hence, they must endure long periods of drought. *Eragrostis trichodes* is the largest bunch grass in the dunes. It is confined to the most favorable habitats on north-facing slopes. Sand dropseed and hairy grama are similar to *Eragrostis* in structure, but differ in size. Sand dropseed, a mid-grass, is most common where the climax grasses are disturbed. Hairy grama, the shortest of the three, is the most abundant on top of the wind-swept dunes and in the ground layer of the sand reedgrass and sand-hill bluestem communities.

The tall grasses with widely spaced stems and rhizomes have deep, well spaced roots. They absorb some moisture in the surface sands where they compete with the short, shallow-rooted bunch grasses, but in addition their roots penetrate 4 to 10 feet in depth and absorb water slowly throughout the growing season. This source of water is a valuable supplement to summer rain, especially during long periods of drought. It is largely for this reason that the tall grasses and many of the shrubs and forbs are able to survive in a region of prolonged summer drought. Redfieldia and Muhlenbergia have roots similar to the tall grasses, but they do not penetrate as deeply, nor do the plants occur where competition with the shallow-rooted bunch grasses is great.

Many successful forbs and small shrubs have root systems similar to the tall grasses in that they penetrate deeply into the sand (Figs. 5, 20, 24, and 27). The chief forbs are *Psoralea lanceolata*, *P. digitata*, *Asclepias arenaria*, *Petalostemon villosus*, *Oenothera serrulata*, *Apocynum cordigerum*, *Lithospermum*

gmelini, and *Sideranthus spinulosus*. All the small shrubs including soapweed, prairie rose, sand cherry, and poison ivy have roots which penetrate 10 to 12 feet deep.

The shallow-rooted forbs are either confined to mesophytic habitats, or they are drought enduring or drought escaping (cf. Shantz 1927). Prairie golden-rod, upland sunflower, and perennial ragweed are confined to the favorable dune habitats. Prairie sage and cacti endure long periods of drought, but the early flowering *Lathyrus stipulaceus*, *Rumex venosus*, *Tradescantia occidentalis*, *Pentstemon angustifolius*, and *Lesquerella ludoviciana* are drought escaping.

BASAL COVER

Plant stems and bunches are widely spaced in sand-hill communities. Basal cover varied from 1 to 3 percent (Table 3). Grasses comprised 85 percent of this cover. Bunch grasses are the most important. For this reason the sand-hill muhley-hairy grama community had a basal cover of 2.7 percent. There was a similar density in the tall-grass communities where blue or hairy grama were present, as in the sand-hill bluestem community (2.2 percent) and the sand reedgrass-blue grama community (1.9 percent). In a pure stand of sand reedgrass, basal cover was only 1 percent.

Blowout grass, sand-hill muhley, sand reedgrass, sand-hill bluestem, and sand-hill sedge have rhizomes 4 to 8 inches in length. Sand dropseed, with rhizomes 2 to 3.5 inches long, grows in open bunches. Sand-hill lovegrass and hairy grama are the only important grasses which grow in dense bunches, and June grass and little bluestem also have this habit of growth. The bunches are widely spaced, and the stems of the rhizome-bearing species are evenly distributed throughout the communities. Among 34 common forbs, 28 species have rhizomes.

SEASONAL ASPECTS

Species contributing to the prevernal aspect are few, and they are not numerous on the dunes. Sand-hill sedge flowers in middle April. *Lathyrus stipulaceus*, *Prunus besseyi*, and *Rumex venosus* are the first plants to unfold conspicuous flowers. They usually appear in early May.

The vernal aspect from middle May to late June is characterized by moderate temperatures and conditions favorable to plant growth. Forbs do not normally grow in sufficient quantity to give color to the landscape dominated by the greens and grays of living and dead grass, but spiderwort and yucca are occasionally conspicuous in disturbed grassland. Western needlegrass, Indian ricegrass, and June grass flower during this period. Most conspicuous among the forbs which flower at this time are *Lesquerella ludoviciana*, *Lithospermum gmelini*, *Pentstemon angustifolius*, and *Tradescantia occidentalis* (Fig. 29).

The estival season begins about June 15 and continues until late July. It is characterized by period-

TABLE 3. A summary of grasses of 25 census and basal area quadrats from each of eight stations from several, typical, well-developed plant communities on Fort Niobrara Game Preserve. It illustrates differences in composition according to variation in soil texture and topography.

	Communities of dune sands										Communities of mixed prairie			
	<i>Muhlenbergia pungens</i> — <i>Bouteloua hirsuta</i>		<i>Andropogon hallii</i> — <i>Bouteloua hirsuta</i>		<i>Eragrostis trichodes</i> — <i>Calamovilfa longifolia</i>		<i>Calamovilfa longifolia</i>		<i>Calamovilfa longifolia</i> — <i>Bouteloua gracilis</i>		<i>Sporobolus cryptandrus</i> — <i>Bouteloua gracilis</i>		<i>Stipa comata</i> — <i>Carex filifolia</i>	
Hygroscopic coefficient.....	0.7		0.8		0.9		1.3		1.0		2.0		4.5	
Topography.....	Top of steep dune		Upper break of steep dune		North-facing dune		South-facing dune		Level area in a dry valley		Level land		Level land	
Criteria.....	Stem counts*	Basal area	Stem counts	Basal area	Stem counts	Basal area	Stem counts	Basal area	Stem counts	Basal area	Stem counts	Basal area	Stem counts	Basal area
<i>Agropyron smithii</i>													241	222
<i>Carex filifolia</i>											(57)	569	(2,950)	5,371
<i>Stipa comata</i>			(7)	18	(18)	32	(16)	70	(61)	78	(114)	639	(527)	5,033
<i>Bouteloua gracilis</i>			(31)	212					(472)	2,955	(583)	5,654	(981)	3,265
<i>Sporobolus cryptandrus</i>	144	137	254	247	195	178	417	359	307	270	3,196	3,171	69	69
<i>Calamovilfa longifolia</i>	361	161	335	169	479	265	3,421	1,540	2,545	1,154	183	87	30	30
<i>Carex heliophila</i>	16	13	407	353	92	79	433	355	203	156	1	4	14	18
<i>Andropogon hallii</i>	75	65	1,171	1,084	64	51	53	43	196	147	18	14		
<i>Bouteloua hirsuta</i>	(335)	2,361	(321)	2,219			(3)	3	(27)	129	(10)	114		
<i>Andropogon scoparius</i>	(47)	842	(170)	805	(7)	16	(3)	20	(1)	1				
<i>Koeleria cristata</i>	(3)	95	(28)	202	(4)	8			(1)	1				
<i>Eragrostis trichodes</i>					(178)	4,330	(36)	279						
<i>Muhlenbergia pungens</i>	4,577	2,806	99	99										
<i>Redfieldia flexuosa</i>	19	7			107	45	1	1						
<i>Cyperus schweinitzii</i>	20	16	4	2	1	1								
<i>Aristida longiseta</i>	(11)	230												
Total basal area.....		6,733		5,410		5,005		2,670		4,893		10,252		14,028
Percent of basal area.....		2.7		2.2		1.9		1.0		1.9		4.1		5.6

*Numbers in parenthesis indicate number of bunches.

FIG. 29. Sand puccoon (*Lithospermum gmelini*) in flower during early June.

ical drought. During the early summer, June grass and needlegrass ripen seed, and sand dropseed, blue grama, and western wheatgrass bear flowers if moisture is sufficient. Most of the sand-hill dominants also bloom when rain occurs. After a heavy rain, flowers of many forbs appear. Most important of these are *Oenothera serrulata*, *Sideranthus spinulosus*, *Argemone intermedia*, *Asclepias arenaria*, *Acerates* sp., *Lygodesmia juncea*, *Apocynum cordigerum*, *Ipomoea leptophylla*, *Liatris squarrosa*, *Petalostemon oligophyllus*, *P. purpureus*, *P. villosus* Nutt., and *Solidago glaberrima*.

The autumnal aspect begins about the first of August. The fall is characterized by rapid shortening of the days and lowering temperatures. The occurrence of timely showers make this a period favorable to plant growth. Though the sand-hill grasses may flower sparingly during the estival season, drought commonly delays anthesis until this period. The most important fall-blooming forbs belong to the Compositae. They are *Chrysopsis villosa*, *Artemisia gnaphalodes*, *A. caudata*, *Aster oblongifolius*, *Machaeranthera canescens*, *Senecio riddellii*, *Kuhnia suaveolens*, and *Ambrosia coronopifolia*.

MIXED PRAIRIE

Mixed prairie occurs on the sandy loams and in transitional zones with Valentine sands where hygroscopic coefficients vary from 2.5 to 4.5 percent.

These soil textures determine the disposal of rain and cause conditions to which the mixed-prairie grasses are most adaptable. There is no runoff on the flat and sandy areas, and moisture penetrates to 5 feet in depth in the fine sandy loam soils. Soil texture and its relation to absorption of rain has more effect upon composition of the mixed prairie than do differences in the aerial environment. The zone of transition between mixed-prairie and dune communities is broad. The presence of *Calamovilfa* in sufficient quantities to be of primary importance marks the transition of the mixed-prairie with the tall-grass communities on the dunes.

SUCCESION AND DEGENERATION

Stages in development of the mixed prairie in abandoned fields on the hardlands illustrate the course of succession. Such fields are first occupied by annuals, chiefly *Salsola pestifer*, *Amaranthus retroflexus* L., *Setaria viridis* (L.) Beauv., *Chenopodium album* L., and *Panicum capillare*. The most important grasses among the early invaders are sand dropseed and western wheatgrass. Wheatgrass is more successful because it propagates by rhizomes. Once a few seedlings are established, increase is so rapid that in a few years wheatgrass occurs in almost pure stands. In the final stages of succession, the short grasses and western needlegrass enter, and western wheatgrass is eventually reduced to a position of minor importance.

Stages in degeneration of pastures in the mixed prairie are shown in Table 4. Needlegrass and niggerwool form the climax community. Three stages in degeneration follow. Under moderate grazing the quantity of needlegrass is reduced, but the growth of

TABLE 4. The total number of bunches (numbers in parenthesis) or stems of grasses in 25 census and basal area quadrats from each of four mixed-prairie communities. Differences in composition and basal cover resulting from grazing and drouth are shown. The first community is climax, and the others represent successive degrees of degeneration.

Plant community →	Needle- grass— niggerwool		Blue grama—niggerwool				Blue grama	
			Station A		Station B			
Species	Stems or bunches	Basal cover sq. cm.	Stems or bunches	Basal cover sq. cm.	Stems or bunches	Basal cover sq. cm.	Stems or bunches	Basal cover sq. cm.
<i>Agropyron smithii</i>	241	222	14	11
<i>Carex heliophila</i>	12	18	1	1
<i>Buchloe dactyloides</i>	(71)	193
<i>Stipa comata</i>	(527)	5,053	(138)	739	28	67
<i>Carex filifolia</i>	(2950)	5,371	(3287)	7,051	(1012)	1,240
<i>Bouteloua gracilis</i>	(981)	3,265	(2025)	12,782	(1640)	8,229	(1773)	7,489
<i>Sporobolus cryptandrus</i>	69	69	3	10	102	99
Total basal cover	13,998	20,584	9,635	7,682



FIG. 30. Western wheatgrass (*Agropyron smithii*) in lowlands on fine sandy loam soils.

niggerwool and blue grama increases. In the second stage of degeneration blue grama becomes completely dominant, and niggerwool disappears. In the final communities under heavy grazing, very open stands of blue grama and an occasional colony of buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.) occur between large patches of unpalatable perennial and annual forbs.

Agropyron smithii.—Western wheatgrass as a postclimax species occupies ravines and areas which receive run-in water (Fig. 30). As a disclimax grass it occupies uplands where the climax grasses have been destroyed by plowing or other disturbances. It invades bare areas rapidly by means of rhizomes, but usually does not mature a crop of seed under the climate of mixed prairie. In the uplands it is unable to compete with blue grama and needlegrass, but in lowlands it attains sufficient height and density to exclude the short grasses.

Western wheatgrass begins development in the middle of April. When moisture is plentiful, it attains a height of 24 to 30 inches by the first of July, but in dry years it is only 6 to 8 inches tall. It becomes semidormant during periods of drought in summer, but renews growth with advent of autumnal rains. An excellent growth was attained in 1938 when nearly 30 percent of the culms bore flowering heads. A dozen quadrats on an area of Brule

clay yielded an average of 1,848 stems, and a similar number of quadrats in a slightly saline meadow in a sand-hill valley had 1,266 stems. Basal cover was 6.1 and 4.2 percent respectively; foliage cover was nearly 100 percent.

Buchloe dactyloides.—Buffalo grass grows neither on the sand dunes nor in the dry meadows but is confined to the hardlands. On the fine sandy loam soils it is present only in the severely grazed pastures where the climax grasses are destroyed. It is also a disclimax species in the broad ravines in the hardlands where western wheatgrass is dominant in fully developed vegetation. On a few areas of Brule clay in the Niobrara Valley and on local areas of Rosebud silt loam soil on the Crookston Table, buffalo grass is an important part of the mixed prairie.

Buffalo grass grows in small bunches which are well spaced as the result of propagation by runners. On the prairie, it seldom attains a height of more than 4 inches. Flowers appear earlier than those of blue grama and usually during the first half of June.

Bouteloua gracilis.—Blue grama is the chief disclimax species in the mixed prairie (Fig. 31). It



FIG. 31. Blue grama (*Bouteloua gracilis*) with small quantities of sand dropseed (*Sporobolus cryptandrus*). Herbaceous plants in the foreground are prairie sage (*Artemisia gnaphalodes*).

forms nearly pure stands under heavy grazing, but occurs only in small quantities with *Calamovilfa* in the broad, dry valleys in the sand hills, and in the climax needlegrass community on the hardlands. It grows as a codominant with sand dropseed where dune sands have been deposited in a thin layer over fine sandy loams. Here the hygroscopic coefficients of the surface sands are 2 to 3 percent, and that of the loamy materials 6 to 18 inches beneath the surface are 4 to 5 percent. In such soils the efficiency of absorption of rainfall by dune sand is combined with high moisture holding capacity of the fine sandy loam.

In this transition zone, sand dropseed and blue grama form climax communities. In an area where the surface sands had a hygroscopic coefficient of 2 percent, blue grama was first, sand dropseed second,

and needlegrass third in amount of basal cover. In a more silty sand with a hygroscopic coefficient of 2.5 percent, blue grama again ranked highest in amount of basal cover, but needlegrass was second, and sand dropseed, third. The number of bunches of needlegrass and blue grama was 60 and 165 percent higher, respectively, in the more silty sand than at the sandier station, but stems of sand dropseed decreased 17 percent.

Blue grama forms low, dense bunches or sods usually 1 to 3 inches in diameter but sometimes 8 to 12 inches. The culms are 12 to 14 inches tall when moisture is plentiful, but usually do not exceed 8 inches during dry years. An average of 4 green leaves with blades 1 to 2 inches in length develop on each culm.

Growth begins late in April or early in May, and the flowering period extends from the last week of June until September, according to the occurrence of rain. Seed production is often light, and for this reason blue grama does not have the pioneer character of sand dropseed. Initiation of root growth from rhizomes occurs during the last two weeks in May. By August the number of roots on each new rhizome ranged from two to six; the average number was three. Mature roots are 4 to 5 feet in length (Fig. 25).

Carex filifolia.—Niggerwool grows in small bunches with needlegrass in climax communities on the hardlands. It is the major species in the ground layer where it attains a height of 3 to 5 inches. In moderately grazed pastures where there are small quantities of needlegrass, growth of niggerwool is increased. Under heavy grazing, however, it is destroyed (Table 4).

Growth begins early in April, flowering occurs late in the month and seeds are usually ripe by the first week in June. The plant becomes dormant in summer but renews growth in autumn when moisture is present. The black roots, which penetrate to a depth of 2 to 3 feet, are stiff, supposedly from large siliceous accumulations (Fig. 32). They remain in the soil many years after the plants have died.

Stipa comata.—Western needlegrass grows on hardlands and in the sand hills where soil texture varied from fine sand to fine sandy loam (Fig. 33). It is dominant, however, only on the fine sandy loam soils where hygroscopic coefficients average 4.5 percent. Bunches of needlegrass in the climax community averaged 9 sq. cm. in basal cover. Twenty-one bunches were present in an average quadrat. At a station on Valentine fine sand, the single bunch averaged 9 sq. cm., and an average of 25 bunches were present per quadrat. Like niggerwool, it begins growth in the prevernal season before the short grasses and thus becomes a successful competitor for soil moisture. It attains sufficient height to shade the short grasses in periods of good rainfall. Its leaves remain curled during summer and fall drought, but upon occurrence of rain quickly revive. Three leaves with blades 12 to 14 inches in length were on each culm. The height of culms averaged 26 to 32

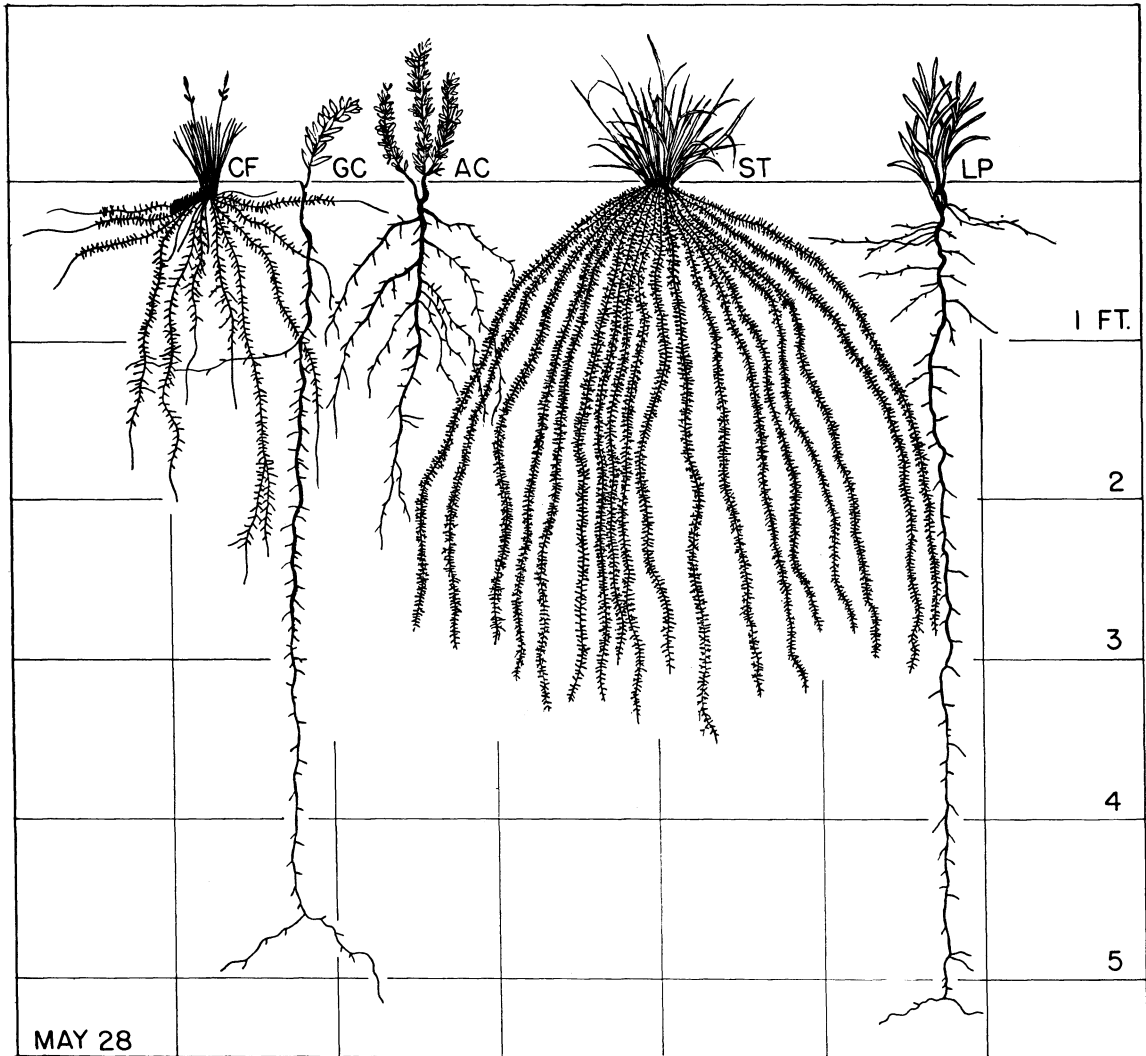


FIG. 32. Bisect in a mixed prairie community on fine sandy loams on the Crookston Table showing root systems of several characteristic grasses and forbs. Niggerwool (*Carex filifolia*) (CF), *Gaura coccinea* (GC), *Artemisia caudata* (AC), western needlegrass (*Stipa comata*) (ST), and *Liatris punctata* (LP).

inches. Few plants had mature seed or yielded much forage without the benefit of early summer rains. In 1936, 1937, and 1939 few seeds formed, but in 1938 a full crop matured. The roots penetrated to a depth of 3 feet (Fig. 32).

The grasses of secondary importance usually occur in disturbed vegetation or they are pioneers on abandoned fields. They are western wheatgrass, sand dropseed, buffalo grass, sand reedgrass, green needlegrass (*Stipa viridula* Trin.), tumblegrass (*Schedonardus paniculatus* (Nutt.) Trelease), and red three-awn grass (*Aristida longiseta* Steud.).

FORBS OF MIXED PRAIRIE

Most perennial forbs of the mixed prairie increase under moderate disturbance caused by grazing. They are most common in areas which receive runoff water.

The most important are: *Pentstemon albidus* Nutt., *P. grandiflorus* Nutt., *Kuhnia suaveolens*, *Echinacea pallida* (Nutt.) Britton, *Liatris punctata* Hook., *Artemisia gnaphalodes*, *Psoralea argophylla*, *Oenothera nuttallii*, *Solidago mollis* Bartl., *S. glaberrima*, *Aster ericoides* L., and *Sideranthus spinulosus*.

Cacti or prickly pear and certain unpalatable perennial forbs and shrubs grow in heavily grazed pastures, where needlegrass and niggerwool have been destroyed and blue grama materially reduced by grazing. They are *Opuntia fragilis* (Nutt.) Haw., *O. humifusa* Raf., *Artemisia caudata*, and *A. frigida* Willd.

Winter annuals are found in disturbed vegetation, especially in communities of blue grama. Sometimes the seeds germinate in the fall and pass the winter in the seedling stage. Often they remain in the soil



FIG. 33. Western needlegrass (*Stipa comata*) with niggerwool (*Carex filifolia*) in a climax community of the mixed prairie undisturbed by grazing.

for several seasons until the environment is favorable to their germination. Winter annuals flower in the spring and early summer. Seed matures about the time hot weather begins. The chief species are *Bromus japonicus* Thumb., *Festuca octoflora* Walt., *Lepidium densiflorum* Schrad., *Plantago purshii* R. & S., and *Lappula occidentalis* (S. Wats.) Greene.

Two biennial species, *Oenothera rhombipetala* Nutt. and *Hymenopappus tenuifolius* Pursh, are confined to very fine sandy soils. *Yucca glauca*, *Artemisia frigida*, *Amorpha canescens*, and *Rosa arkansana* likewise grow on these soils, but are also present in disturbed phases of vegetation on fine sandy loams and occur in areas which receive run-in water.

LAYERING

Well developed communities are characterized by two layers above ground. A group of mid grasses, including needlegrass, western wheatgrass, and sand dropseed, form a layer 18 to 24 inches above a lower one which is composed of blue grama and niggerwool. Several species of forbs are found in both layers.

Root layering is not as obvious in the mixed prairie as in the dune communities, since moisture does not penetrate beyond 4 to 5 feet. There is, however, a concentration of roots near the surface. The root systems of blue grama, needlegrass, and niggerwool

penetrate to a depth of 3 to 4 feet (Fig. 32). Forbs have taproots which approximate the same depth. Roots of cacti are shallow (Fig. 25).

SEASONAL ASPECTS

The greatest growth in mixed prairie was made in spring. Summer rains are too light and infrequent to supply moisture in sufficient quantity to sustain much growth. Inefficient absorption by the soil also causes much loss of water by runoff. Autumn is usually a period of revival.

Flowering in the mixed prairie occurred mainly in spring and autumn. The time of revival in spring is important in survival and dominance. The grasses which begin growth in the prevernal season and flower before the drought are the climax species. Those which are slow to renew growth and flower in early summer or midsummer are mostly disclimax species.

Needlegrass and niggerwool are effective competitors for moisture because they begin growth early in spring and mature seed prior to the occurrence of prolonged drought. Western wheatgrass, the dominant in lowlands, also begins growth during the prevernal season, but may not flower until July. It seldom bears a crop of seed. This type of reproduction, however, is of little importance to western wheatgrass because it propagates extensively by long rhizomes. Blue grama renews growth later than the other climax species, but it flowers at about the same time as western wheatgrass. Buffalo grass renews growth in spring at the same time as blue grama, but it flowers in early June. Time of anthesis, however, depends upon occurrence of rain. Blue grama may flower as late as the middle of September.

In the vernal aspect the most conspicuous flowers are those of *Malvastrum coccineum*, *Gaura coccinea*, *Pentstemon grandiflorus*, *P. albidus*, and *Cheirinia aspera*. Those which bloom in the late summer and fall are *Liatris punctata*, *Aster ericoides*, *Artemisia caudata*, and *A. frigida*.

BASAL COVER

The climax community on the hardlands had somewhat higher basal cover (5 percent) than those of the sand hills. Moderately grazed pastures, where blue grama and niggerwool were dominant, had a basal cover of 8 percent. This was a reaction of the short species to a decrease in competition with needlegrass. In severely grazed areas, however, basal cover was considerably less. At a station which was dominated by blue grama but which had a few plants of niggerwool, the basal cover averaged 3.4 percent; in a poor stand of blue grama, the basal cover was 3.0 percent.

WOODLAND

There are approximately 10,000 acres of woodland in Cherry County. Trees, shrubs, and a relic, herbaceous flora meet in postclimax communities in the river valleys. The deciduous trees grow in well

aerated soils where moisture is available from a stable water table throughout the year. Woodlands are common in the deep canyons and immediately along the streams, but the broad river valleys are usually occupied by scattered groves of trees alternating with chaparral and tall-grass meadow. The ecotone between the deciduous woods and the mixed prairie on the hillsides is narrow because of marked changes in depths to the water table. The largest and best developed deciduous woodland is found along the south side of the Niobrara Valley for a distance of 25 miles east of Valentine.

Ponderosa pines grow with other Rocky Mountain plants on rough, stony land where run-in water is received from rock surfaces and where snow lodges during the winter. They are located well above the water table and must withstand varying periods of drought. Seedlings do not become established on broad, gentle slopes because the grasses are better equipped to obtain the available moisture. Shade in the deciduous woodland is too great for their development.

Most of the timber was cut by the early settlers 50 to 60 years ago. Since then the coniferous trees have reproduced from seed, and much second growth of deciduous trees has developed from the stumps. Since fire has been under control, trees have advanced into the chaparral and grasslands as far as the environment permitted. Because deciduous trees are able to grow only where their roots have access to a permanent water table, there was little loss from drought. Ponderosa pine is especially resistant to drought, and only rarely were trees killed. But in a few dry canyons, which did not have a favorable water supply, mortality of the chaparral was as great as 85 to 95 percent.

The deciduous woodland is composed largely of flood-plain species, but a few trees which usually grow on the valley hillsides in the eastern part of Nebraska occupy the more xeric habitats in the flood plain. Sandbar willow (*Salix interior* Rowlee) grows on sands recently deposited along the Niobrara River. Peach-leaved willow (*Salix amygdaloides* Anders.) and Sargent's cottonwood (*Populus sargentii* Dode) are the chief trees on more stabilized river sand. Most of the flood plains and river banks, however, have not been disturbed for a long time. The dominants of the flood plains are the chief species. They include American elm (*Ulmus americana* L.), green ash (*Fraxinus lanceolata* Borkh.), red ash (*Fraxinus pennsylvanica* Marsh.), box elder (*Acer negundo* L.), and hackberry (*Celtis occidentalis* L.) (Fig. 34).

Ironwood (*Ostrya virginiana* (Mill.) K. Koch) and paper birch (*Betula papyrifera* Marsh.) grow about springs on the north-facing hillsides east of Valentine. A small stand of *Populus tremuloides* Michx. was also found in this habitat. Bur oak (*Quercus macrocarpa* Michx.), elm, ash, box elder, and red cedar (*Juniperus virginiana* L.) occur on these slopes where ground water is probably present in only small amounts at certain periods during the summer months.



FIG. 34. View of deciduous woods in Niobrara Valley. The major tree is American elm (*Ulmus americana*). The grass in the foreground is *Elymus villosus*.

Shrubs grow beneath the trees and along the margins of woodlands, and sometimes form stands several acres in extent in the broad flood plains and on the steep, north slopes of dunes. The chief shrubs are choke cherry (*Prunus melanocarpa* (A. Nels.) Rydb.), buckbrush (*Symphoricarpos occidentalis* Hook.), wild plum, golden currant (*Ribes odoratum* Wendl.), prairie rose, poison ivy, Macoun's rose, and lead plant. Buffalo berry (*Shepherdia argentea* Nutt.) and sumac (*Rhus glabra* L.) occupy similar habitats but are of minor importance.

Shrubs confined to the habitats immediately along river banks and edges of swamps are dogwood (*Cornus interior* Rydb.), black currant (*Ribes americanum* Mill.), blue indigo (*Amorpha fruticosa* L.), and Missouri willow (*Salix missouriensis* Bebb.).

Three species of vines in open woodlands are wild grape (*Vitis vulpina* L.), Virginia creeper (*Parthenocissus quinquefolia* Planch.), and bittersweet (*Celastrus scandens* L.). Bittersweet is a twiner but the other two have tendrils.

Grasses and forbs in the moist woodlands have a foliage cover of nearly 100 percent, except in the most shaded portions and in the driest parts. The vernal aspect is dominated by *Carex sprengei* Dewey, and that of summer by *Elymus villosus* Muhl. and *E. virginicus* L. Disclimax phases of woodlands are dominated by annual weeds, chief of which are

Chenopodium album, *Collomia linearis* Nutt., *Lappula virginiana* (L.) Greene, and *Parietaria pennsylvanica* Muhl.

Hackberry forms small groves with only a few to as many as 100 trees in the hollows (old blowouts) on north sides of dunes and in river valleys. The trees on the lower edge of the grove at Hackberry Lake probably have access to the water table 10 to 15 feet beneath the surface. Here they attained a height of 24 to 30 feet. Trees on the upper edge were only 8 to 10 feet high. The ages of these trees, which were determined by the use of an increment borer, ranged from 33 to 45 years and averaged 40 years. Diameters at breast height (D. B. H.) averaged 5 inches. Distances between trees varied from 4 to 10 feet, but two trunks commonly grew together. The crowns of the trees formed nearly a complete cover. Shrubs and herbs grew beneath the hackberry trees where stock was excluded.

Bur oak is at its western limit in the Niobrara Valley 15 to 20 miles west of Valentine. It becomes shrub-like and attains a height of only 15 to 20 feet where moisture is limited. The trunks have a diameter of 2 to 7 inches. Where an abundant supply of ground water was available, the trees were 40 to 50 feet tall. Some of the mature trunks were 21 to 34 inches thick (D. B. H.), and the trees were 200 to 250 years old. Most of them, however, were less than 50 years of age and had a diameter of only 12 to 18 inches.

Red cedar grows in scattered stands throughout the deciduous woodlands and occurs in pure stands locally, especially in the shallow valley near the headwaters of Schlegel Creek. Here it forms a transition zone 2 to 3 miles in length between the deciduous woodlands in a deeper portion of the valley and chaparral in a shallower one. It also grows in pure stands on the upper edge of the deciduous woodlands in a zone of transition to ponderosa pine. The tallest trees were 25 to 30 feet high and 30 to 40 years old.

Ponderosa pine is usually found on rough, stony lands where water runs in from rock surfaces (Fig. 35). Continuous stands of pine grow along the edge

of the Crookston Table on exposures of the Ash Hollow limy sandstone formations from Valentine eastward to Springview in Keya Paha County. A growth of pine on the south side of Niobrara Valley east of Valentine and on both sides of the valley from Valentine westward through Sheridan County occurs only in isolated stands. A continuous stand grows on the canyon walls of Schlegel, Gordon, and Snake valleys. Probably all habitats favorable to the growth of pine seedlings are now occupied by established trees, and little opportunity remains for enlargement of stands through natural propagation.

The average age of 120 trees of ponderosa pine at three stations near Valentine was 44 years. The average height was 25 feet, and the average D. B. H., 8 inches. Certain pines were isolated while others were only a few feet apart. Average distance between trees in two groves was 7 feet. Branches of pine trees 40 to 50 years of age overlapped those of adjacent trees when the trunks were less than 15 feet apart. A tree more than 175 years of age, observed at Fort Niobrara Game Preserve, had a D. B. H. of 33 inches and attained a height of 70 feet. Another tree 24 inches in diameter and 75 feet tall was over 103 years old. Only 17 percent of the trees were under 25 years of age. Little reproduction has taken place during the past 20 years.

Ponderosa pine has been successfully planted on both the hardlands and the sand hills. An excellent example of the growth of pine on dune sands is found in the Nebraska National Forest. A planted grove 30 years old on a hardland area had an average height of 24 feet and a D. B. H. of 7 inches. Growth of red cedar from planted seedlings has also been successful.

The most important shrubs associated with ponderosa pine are white sage, soapweed, fetid sumac (*Rhus trilobata* Nutt.), poison ivy, prairie rose, sand cherry, western choke cherry, and match weed (*Gutierrezia sarothrae* (Pursh) Britton and Rusby).

SUMMARY

The sand-hill region in Nebraska is grassland with a variety of habitats caused by differences in soil and sand textures, drainage, and topography.

The annual average rainfall is 18 inches. High temperature, low humidity, prevailing south wind, and frequent drought are unfavorable to plant growth through a part of the summer. Greatest growth is made in spring and fall.

Sand efficiently absorbs moisture. There is no runoff, and loss by evaporation from the surface is small. Fine sandy loams are less efficient in absorption of rain. Efficiency of absorption is especially important during the critical months of summer and is the major cause for differences in composition of vegetation on the several textures of soil on the uplands. Topography also modifies aerial environment and causes local differences in composition of vegetation, especially in the sand hills.



FIG. 35. Ponderosa pine alternating with the mixed prairie on rough, stony land in the Niobrara Valley. The deciduous trees are bur oak.

Sampling of soil for moisture showed that pioneer communities use available moisture over a longer period of time than the climax communities. Vegetation on the fine textured soils withstood longer periods of drought than that in the sand dunes.

The tall grasses in the subirrigated meadows and the deciduous trees along the rivers have more available moisture than is afforded by rainfall because roots of these postclimax species receive moisture from the ground water.

Seasonal and daily fluctuations of the water table in the meadows result from trans-seasonal evaporation, and amount of water supplied by springs and seepage.

Drainage materially affects the amount of periodic fluctuation. Greatest fluctuations occur in the poorly drained lakes. Well drained lakes maintain a constant level in years of high rainfall; water from springs prevents marked lowering during drought.

River water has little salt in solution. Well drained lakes and swamps have fresh water; poorly drained lakes are saline.

Highest temperatures are on south slopes of dunes and in the prairie of hardlands. Environment on north slopes of the dunes and valleys is ameliorated by lower temperatures, less insolation, and protection from prevailing south winds.

Evaporation is highest on the tops of the dunes and lowest in the meadows and woodlands.

Submerged, floating and emersed aquatic plants are present in the fresh-water lakes and swamps. The chief plants are species of *Potamogeton*, *Myriophyllum*, *Ceratophyllum*, *Typha*, *Sagittaria*, *Scirpus*, and *Phragmites*.

Saline lakes have only a growth of algae. *Distichlis stricta* and *Scirpus americanus* grow on the shores and in the saline meadows.

Mesophytic tall-grass communities in the subirrigated meadows occur in three zones. A lower zone is flooded during the early part of the growing season. It is occupied by sedges (*Carex* spp.) and hydrophytic grasses, chiefly *Calamagrostis*. A middle zone is never flooded but water is near the surface throughout the year. Here tall grasses (*Spartina pectinata*, *Panicum virgatum*, *Sorghastrum nutans* and *Andropogon furcatus*) are dominant. The grasses in the upper edge of the meadow are too far above the water table to have access to ground water in autumn. They are dominated by true-prairie grasses and forbs.

Postclimax grasses grow on the dunes. *Redfieldia flexuosa* and *Muhlenbergia pungens* are pioneers in the blowouts. *Muhlenbergia* is a pioneer and persists in overgrazed dunes. *Andropogon hallii* is often a pioneer in blowouts and occurs only in small communities as fully developed vegetation. *Eragrostis trichodes* is able to dominate the north side of dunes in winter pastures, but, along with *Andropogon*, it is materially reduced as the result of selective grazing in most year-long pastures. *Calamovilfa longifolia* and *Sporobolus cryptandrus* are the most important range grasses. *Bouteloua hirsuta* and *Carex helio-*

phila are present, especially in the ground layer of mature communities.

Three stages in degeneration under grazing are evident. The most palatable grasses, such as *Andropogon hallii*, *Eragrostis trichodes*, and *Panicum virgatum*, are selectively grazed. *Calamovilfa longifolia* and *Sporobolus cryptandrus* become the dominant grasses in the second stage. In a third stage *Muhlenbergia pungens* and certain weedy forbs are common.

Ecological relations of the dominant grasses and forbs were understood only after the roots were studied. *Redfieldia flexuosa*, *Muhlenbergia pungens*, *Andropogon hallii*, and *Calamovilfa longifolia* have roots 4 to 8 feet deep and form an open growth by means of rhizomes 4 to 8 inches in length. All are tall grasses except *Muhlenbergia pungens*. It has essentially the same ecological position in its community with *Bouteloua hirsuta* as the tall grasses have in their respective communities.

The bunch grasses have shallow, but much branched roots. They spread widely in the surface soil but seldom penetrate more than 18 inches into the sand. *Eragrostis trichodes* forms tall bunches, *Sporobolus cryptandrus* is a mid grass, and *Bouteloua hirsuta* is a short grass. Short grasses form the major portion of the ground layer.

Forbs are of minor importance. Five major species are *Tradescantia occidentalis*, *Lygodesmia juncea*, *Artemisia gnaphalodes*, *Ambrosia coronopifolia*, and *Psoralea lanceolata*. These species are either drought enduring or drought escaping. Certain others are present only as pioneers in undeveloped communities where competition for moisture is not great. Some unpalatable species thrive in overgrazed pastures.

The bunches and stems of both grasses and forbs are widely and evenly spaced in the several communities. Basal area ranged from 1 to 3 percent.

The grass dominants flower in summer or fall, but growth takes place throughout the season according to occurrence of rain. Reactions to summer showers are more evident on the dunes than in the hardlands because of the differences in efficiency of absorption of water. The forbs bloom chiefly in spring and fall.

Five mixed-prairie grasses dominate fine sandy loam soils. The climax species are *Stipa comata* and *Carex filifolia*. *Bouteloua gracilis* increases greatly under grazing, *Buchloe dactyloides* is present only in overgrazed pastures. *Agropyron smithii* dominates the ravines where run-in water is received. It is a pioneer on abandoned fields.

Three stages in degeneration of mixed prairie are evident. *Stipa comata* is the first grass to disappear. In a second stage of degeneration *Carex filifolia* is destroyed and *Bouteloua gracilis* becomes dominant. In the final stage *B. gracilis* and *Buchloe dactyloides* are present with a large number of unpalatable forbs.

The chief forbs are *Aster ericoides*, *Artemisia caudata*, and *Listris punctata*. Other species such as *Artemisia frigida* and *Opuntia* spp. increase under heavy grazing.

Agropyron smithii and *Stipa comata* are mid

grasses; the others grow in short bunches. The mid grasses and *Carex filifolia* begin growth very early; the short grasses revive later. Greatest growth is made in spring. Flowering of the climax grasses takes place in May, and seeds are mature before mid-July. *Agropyron smithii* and *Bouteloua gracilis* flower in midsummer or later according to occurrence of rain.

Root layering in mixed prairie is not as evident as it is on the sand dunes. Roots penetrate 4 to 5 feet deep in the fine sandy loams. Basal cover was approximately 5 percent in climax vegetation (mixed prairie) but only 2 to 3 percent in disclimax communities of this association.

Ulmus americana, *Fraxinus lanceolata*, *Acer negundo*, and *Populus sargentii* are the major deciduous trees which grow along the banks of the river. Ponderosa pine occurs on the rough, stony lands in the valleys. Mixed prairie, true prairie, and certain Rocky Mountain shrubs and forbs alternate with the pine and often form an understory.

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